

Disturbance and Refugia in the Ecology of Stream Benthic Communities

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**Disturbance and Refugia in the Ecology
of Stream Benthic Communities.**

by

Charlotte Gjerløv

A thesis submitted for the degree of Doctor of Philosophy

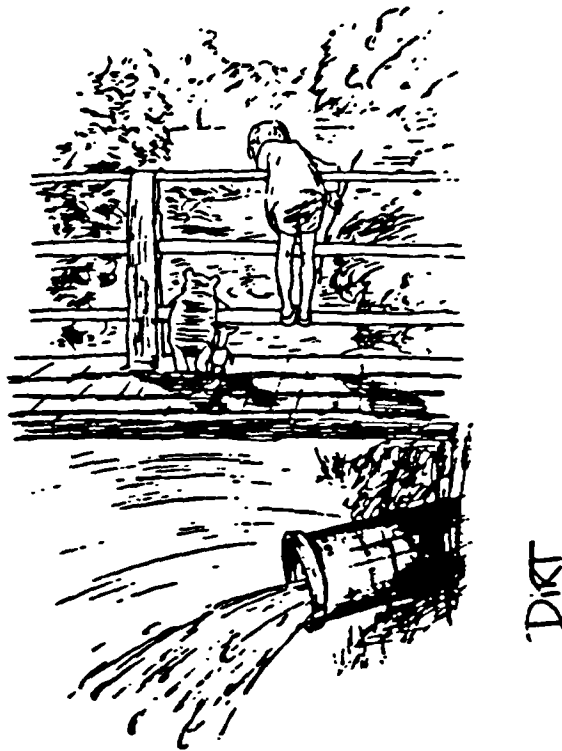
**School of Biological Sciences
Queen Mary and Westfield College
University of London**

1997



Til mor og far.

Site 27: Pooh Sticks Bridge



"Well, it's not my stick!" exclaimed Piglet

Private Eye 931, 22-8-97

Abstract

Natural habitats are spatially and temporally heterogeneous and exert powerful influences over the distribution, interactions and adaptations of organisms. Southwood's (1977, 1988) Habitat Templet was tested in twenty-two streams, using refugium availability and disturbance frequency as the two axes. Disturbance frequency was estimated as the number of days a year 50% of the stream bed was in movement, and refugium availability was estimated from shear stress frequency distributions using FST hemispheres

A long-term sampling regime allowed persistence to be estimated in all streams. A comparison of sites revealed that all sites were approximately equally persistent, and no pattern was found with disturbance frequency or refugium availability. This suggested that some degree of adaptation to the habitat had occurred, and differences in species traits were consequently investigated.

Extensive literature reviews were assessed to obtain traits for as many of the species as possible in the Ashdown Forest. Species traits were compared to environmental variables using multivariate statistics. Only weak patterns were shown, although one of the traits that was significantly different between sites was mobility. It is believed that the concept of 'trade-offs' between traits and the constant problem faced by ecologists of scale are the causes of this poor correlation.

It is generally believed that frequently disturbed streams will have a higher proportion of mobile species to enable rapid recolonisation. Extensive field experiments revealed that there was indeed a difference between streams, but that communities in less disturbed streams were actually more mobile than those in disturbed streams.

Disturbance frequency and refugium availability did not significantly contribute to explaining species variance at a large scale, but differences in mobility were revealed at a smaller scale. These results suggest that Southwood's Habitat Templet Theory may be important, but care must be taken when choosing the scale at which it is tested.

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CHAPTER 1: General Introduction.

It is a basic aim of ecology to understand the relationship between the enormous variety of organisms and the environment in which they are found. Natural habitats are characteristically heterogeneous in both time and space (Sousa, 1984), and these spatiotemporal variables exert powerful influences over the distribution, interactions and adaptations of organisms (Southwood, 1977, 1988). In order to describe and predict patterns of distribution and abundance of organisms, ecologists must first understand the influence that the habitat exerts upon them.

1.1 Habitat Templet Hypothesis

Southwood realised the need for a framework on which to base predictions about the characteristics of species and communities, and in 1977 he developed the Habitat Templet Hypothesis. The hypothesis states that the habitat acts as a templet for species traits, i.e. "the habitat provides the templet upon which nature forges characteristic life-history strategies". On an evolutionary timescale the spatiotemporal variations of the habitat act as selective forces on the organisms living in them, leading to adaptations to the environment by the evolution of species traits that maximise fitness. In ecological time the habitat acts to filter out unsuccessful strategists amongst colonisers, thus controlling community composition.

Although it may not be possible to create an ecological "Periodic Table", as Southwood suggested, the Habitat Templet provides a much needed framework on which to base questions, predictions and testable hypotheses.

1.2 Axes labels

The success of the templet depends on defining axes that relate to the temporal and spatial scales relevant to the organisms of interest. The physical habitat characteristics chosen as axes labels must be of overall importance to the organisms

considered. Southwood himself suggested that the axes of the templet should reflect heterogeneity in time and space.

It is now widely recognised that disturbance may play an important role in structuring communities (Sousa, 1984; Pickett & White, 1985; Resh *et al*, 1988; Townsend, 1989; Reice *et al*, 1990; Hildrew & Giller, 1994). An obvious disturbance in streams is that associated with high flow. Although spates may increase the density-independent mortality of invertebrates (Niemi *et al*, 1990; Giller *et al*, 1991), communities are persistent and recolonisation is often rapid (Badri *et al*, 1987; Scrimgeour *et al*, 1988). This suggested the presence of in-stream flow refugia, defined as areas where invertebrates may take refuge during the flow, thus avoiding being washed out of a favourable habitat, and enabling rapid recolonisation after the event.

In streams, therefore, appropriate axes labels for the Templet would be disturbance frequency, which can be described as temporal heterogeneity, and refugium availability, which has been expressed as spatial heterogeneity (Townsend & Hildrew, 1994).

1.3 Templet predictions

Townsend & Hildrew (1994) proposed a templet with axes of disturbance (estimated by temporal heterogeneity) and refugium availability (spatial heterogeneity). They reasoned that increased refugium availability would ameliorate or modify the influence of disturbance. In the event of disturbance, populations may exhibit resilience (the ability rapidly to return to pre-disturbance densities) or resistance (the ability to withstand the effect of disturbance without loss). Along the disturbance axis, species with resilience traits (such as high mobility, short life cycles, small size, rapid reproduction) and resistance traits (such as streamlining, hooks and suckers for firm attachment) were predicted to increase in importance. The greater the refugium availability, the more would the effect of disturbance be reduced, so that

species lacking resilience/resistance traits might still persist under moderate disturbance regimes.

1.4 Thesis aims

The aims of this thesis were, therefore, to test the Habitat Templet Hypothesis on a number of streams. The axes of the templet are defined as disturbance frequency and refugium availability. An account of how these were measured is given in Chapters 3 and 4.

Chapter 5 addresses the question: are communities in streams equally persistent, independent of disturbance frequency and/or refugium availability? One might expect to see greater fluctuations, and thus lower persistence, in highly disturbed streams with a low refugium availability. If streams are equally persistent, however, then this could suggest that the communities consist of component species with adaptive traits appropriate for the environment concerned.

Differences in resilience/resistance traits (Townsend & Hildrew, 1994) are tested in Chapter 6. Is there a greater proportion of organisms with these traits in streams with a higher disturbance frequency and/or low refugium availability? One might expect resistance traits to be more prominent in disturbed streams lacking flow refugia, than where refugia are present. If avoiding the forces of the flow is impossible, the only option to limit the effect of the flow is to avoid being washed away in the first place, i.e. by being streamlined or having suckers, hooks or other mechanisms. Similarly, resilience traits are usually associated with refugium use.

Finally, Chapter 7 examines one specific resilience trait, high mobility. In frequently disturbed streams one would expect a greater proportion of organisms with high mobility. This would enable rapid colonisation after a disturbance event. Are denuded substrata colonised more rapidly in frequently disturbed streams? And what is the relationship with refugium availability?

CHAPTER 2: Site Description.

2.1. Site description

The work was carried out in a number of streams in the Ashdown Forest, East Sussex, southeast England (National Grid Reference: TQ 520300) (Fig. 2.1). The thirty sites shown on the map are sites that have previously been worked on by other members of the laboratory (Townsend *et al*, 1983; Townsend *et al*, 1987; Edmonds-Brown, 1995), and therefore substantial amounts of data were available. Of the 30 sites, 26 were chosen for further study. This number was further reduced during the experimental period for various reasons. See explanations in the text at the appropriate time.

The streams are the headwaters of two rivers; the River Medway runs north into the Thames estuary, and the River Ouse runs south to the English Channel. The forest itself is an area of common land situated in the centre of the Weald and underlain by the Ashdown Sands (a soft, fine sandstone). At higher altitudes the 'forest' vegetation is typical of acid heath land; it is dominated by *Calluna vulgaris* and *Erica* sp., although in parts bracken (*Pteridium aquilinum*) dominates.

The sites were numbered in the original survey (Townsend *et al*, 1983), so that sites 1-15 (and site 35 added later) were found in the upper reaches, and sites 16-29 further downstream. Sites 30-34 were below small impoundments. In most upstream sites the streams run through mixed woodland consisting mainly of Alder (*Alnus glutinosa*), with Oak (*Quercus robur*), Beech (*Fagus sylvatica*), Birch (*Betula pendula*), Holly (*Ilex aquifolium*) and Hazel (*Corylus avellaria*). Generally the downstream sites are lined with trees, although the streams mostly run through pasture land. The downstream sites are also generally closer to roads, sometimes actually running over or under them (site 14, 21, 34, 29 and 26).

Most of the streams have a coarse or fine gravel substratum, although there are a few exceptions. This will be discussed in greater detail in Chapter 3. All streams have a similar slope (between 1 and 1.5°). Many of the streams in the forest have a low pH (Table 2.1). This is partly due to the acidic rain and poor buffering capacity of

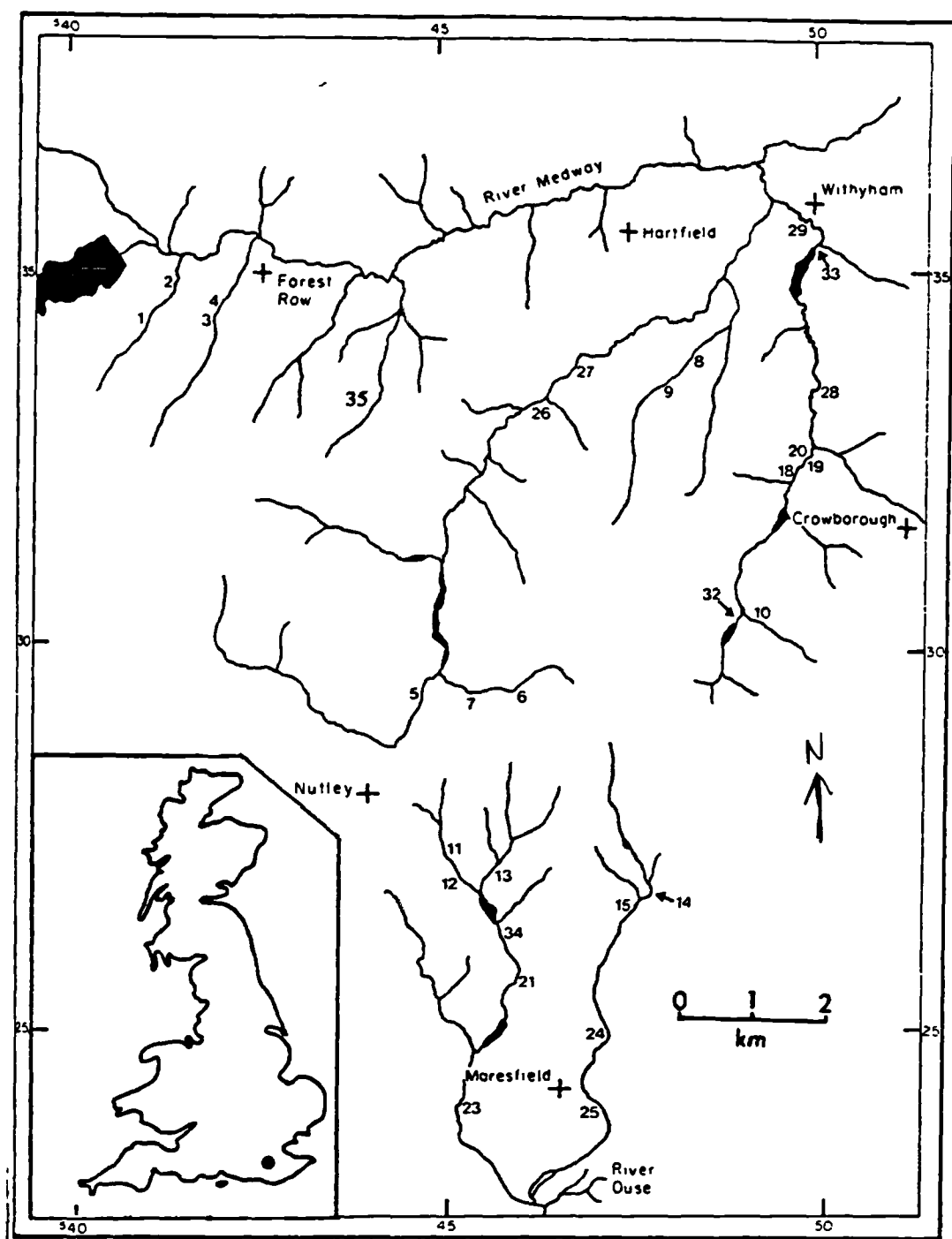


Figure 2.1. Map of the Ashdown Forest, East Sussex, Southeast England, showing the location of 30 stream sites. (National Grid Reference: TQ 520300) (Adapted from Groom, 1987).

Table 2.1. Table of sites numbers, names, pH and distance from headwater.
(Townsend *et al*, 1983).

Site number	Site name	Distance from headwater (km)	Range of pH
1	Lavender Platt	0.61	4.5-6.0
2	Weirwood Road	1.75	5.6-6.8
3	Kidbrooke Park (i)	1.77	4.3-6.1
4	Kidbrooke Park (ii)	1.82	4.1-5.7
5	Nutley Bridge	3.90	4.4-6.8
6	Old Lodge (i)	1.72	3.6-5.6
7	Old Lodge (ii)	2.40	4.2-6.8
* 8	Chuck's Hatch	2.10	4.6-6.5
9	Lone Oak	1.82	3.8-5.7
10	Crowborough Warren	1.27	5.4-6.5
* 11	Nutley	0.56	5.6-6.6
12	Cackle Street	1.21	5.1-6.8
13	Dodd's Bottom	1.64	4.1-6.4
* 14	Old Lands	1.80	5.3-6.4
15	Fairwarp	2.58	5.5-6.9
18	Marden's Hill (i)	4.73	5.0-6.3
19	Marden's Hill (ii)	4.83	4.6-6.5
20	Below Friar's Gate	5.41	5.0-6.3
21	Old Forge	3.19	5.5-7.0
23	Batt's Bridge	6.05	5.3-7.4
24	Hendall	3.14	5.4-7.1
25	Maresfield	5.29	6.4-7.8
26	Marsh Green	9.54	4.4-6.8
* 27	Pooh Stick's Bridge	11.08	5.1-7.0
28	Half Moon Inn	6.30	5.6-7.4
29	Withyham	9.29	5.4-6.7
32	Clockhouse Lane	2.13	4.5-6.0
33	Withyham Green	8.22	5.4-7.0
34	Boringwheel Mill	2.35	5.3-7.1
35	Broadstone Stream	0.58	4.0-6.2

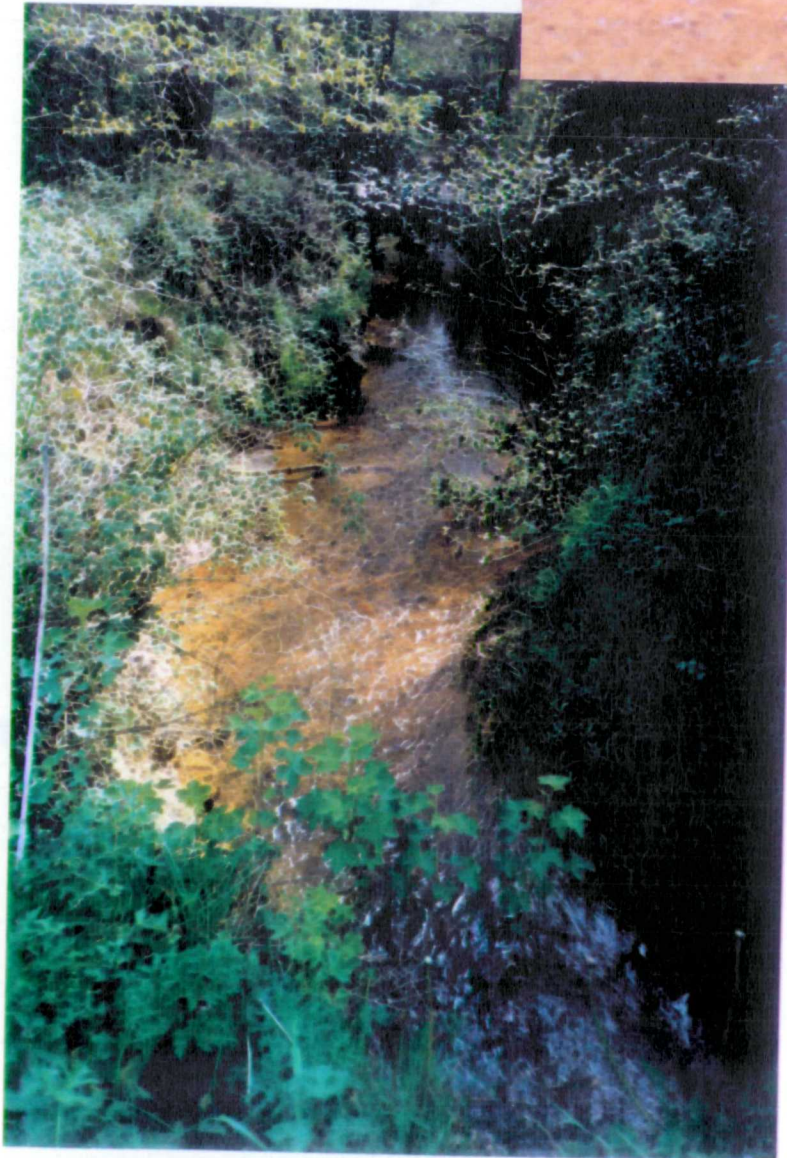
* indicates sites on which no further work was carried out. These sites were either difficult to access (8 & 14), did not have a stony substratum (27) or were subjected to frequent human and canine disturbances (11).

the sandstone, and partly because of drainage through *Sphagnum* moss at some springs (Townsend *et al*, 1983). Many of the acid streams in periods of low flow have an ochre layer covering the substratum (Plate 2.1). This is a result of deposits of the iron bacterium *Leptothrix ochraceae* and ferric hydroxide, which is derived from the iron-bearing rocks of the area (Hildrew & Townsend, 1976). From the Roman era until the 18th century there was a busy iron industry in the Ashdown Forest, which resulted in much tree-felling. Evidence of the industry can still be found at Marden's Hill, where a lake and mill were created, and the ruins of the dam and overflow remain largely untouched.

The invertebrate assemblage in the streams varies most significantly with pH (Townsend & Hildrew, 1983; Edmonds-Brown, 1995), but also with the presence or absence of fish. Fish are acid intolerant, and are generally excluded from the most acid streams. Acid-sensitive invertebrates include the Ephemeroptera, *Gammarus* sp. and most Mollusca. The invertebrate assemblage in Broadstone Stream, an acid stream, is dominated by Plecoptera (*Nemurella pictetii* and *Leuctra nigra*) and Trichoptera (*Plectrocnemia conspersa*). Circumneutral streams have a greater variety of taxa, most notably Ephemeroptera, molluscs, oligochaetes, Chironomidae and *Gammarus pulex*.

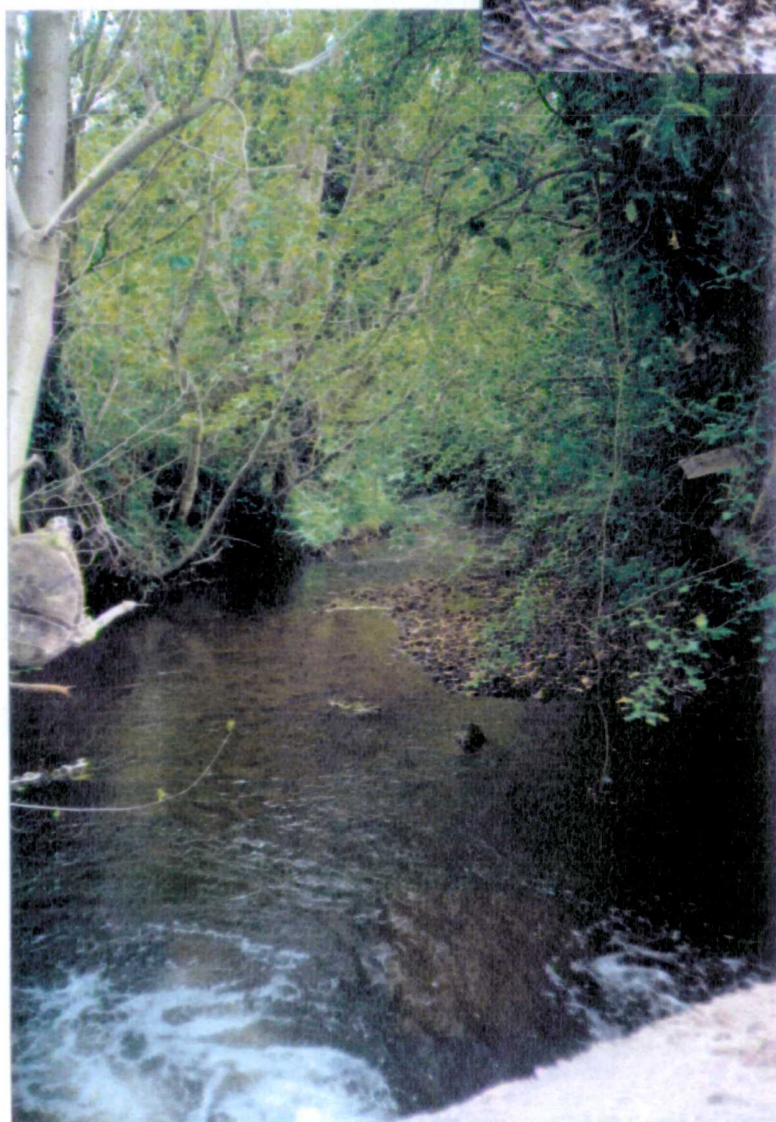
It is evident that the physical habitats vary greatly between the streams. Some streams, such as Broadstone Stream (Plate 2.2) and Kidbrooke Park, are sluggish and have a large quantity of woody debris in them. Both of these sites also have many tree roots in the stream channels, contributing to the stream bed heterogeneity. Other streams, such as Batt's Bridge, Marsh Green (Plate 2.3) and Weirwood Road, have relatively uniform sediments and straight channels with very little if any woody debris or trees extending into the channels. Boringwheel Mill has patches of high shear stress and a ^{broken}slatelike substratum (Plate 2.4). Clearly the difference in channel morphology and hydrology will be important to the invertebrates.

Plate 2.1. Below Friar's Gate



**Plate 2.2. Broadstone Stream
and Old Forge**

Broadstone Stream



Old Forge

**Plate 2.3. Batt's Bridge and
Marsh Green**

Batt's Bridge



Marsh Green

**Plate 2.4. Boringwheel Mill
and Withyham**

Boringwheel Mill



Withyham



2.2. Previous studies

During the last twenty years these streams have been the focus of extensive research. Many studies have involved intensive studies at just one or two sites, but a few have involved the whole suite of sites.

2.2.i. Intensive studies- same stream (Broadstone Stream)

(species-poor)

Due to its relatively simple fauna Broadstone Stream has been subjected to intensive studies. Early work focused on drift (Townsend & Hildrew, 1976) and predator-prey interactions of the two main predators, *Plectrocnemia conspersa* and *Sialis fuliginosa*, and their prey (e.g. Hildrew & Townsend, 1976, 1980, 1982; Townsend & Hildrew, 1978, 1979, 1980; Lancaster *et al*, 1988; Schofield *et al*, 1988). Lancaster *et al* (1990, 1991) while attempting manipulations to demonstrate the effects of predation found that patchiness and mobility of prey complicated the results, and this led to the suggestion that such interactions might be difficult to detect on a small scale, but might be more apparent on larger areas of stream bed.

Shortly after this studies began on the physical patchiness of the stream bed. Measurements of shear stress revealed that patches of low shear stress existed which could persist throughout the discharge hydrograph (Lancaster & Hildrew, 1993a). Further studies revealed that during high discharge animals accumulated in these hydraulic 'dead zones', thus effectively using them as flow refugia (Lancaster & Hildrew, 1993b). The proportion of low shear stress areas in a stream channel may also affect the distance organisms are transported in the drift (Lancaster, Hildrew & Gjerløv 1996, see Appendix 1).

2.2.ii Extensive surveys

Townsend *et al* (1983) conducted an extensive survey of 34 streams in 1976 in an early attempt to relate community structure to environmental variables. They found that pH was of overall importance in determining community structure, and that low pH sites generally had low species richness and low abundance. This study

was followed up in 1984 (Townsend *et al*, 1987) and 1989-90 (Edmonds-Brown, 1995) in 27 and 26 streams respectively. These surveys found a similar relationship between community structure and environmental variables and were furthermore able to make a comparison of long-term persistence between sites. Townsend *et al* (1987) found a trend towards higher persistence in cool, low pH, upstream sites.

CHAPTER 3: Substratum analysis and disturbance frequency.

3.1 Introduction

For much of this century, during which the discipline of community ecology developed, it has been believed that species interactions, such as inter- and intraspecific competition and predation, are the overriding factors determining the structure of species assemblages (e.g. Cody & Diamond, 1975; McIntosh, 1985; Case & Diamond, 1986). This views communities as essentially equilibrial systems that require a largely constant environment. In many habitats, however, and in streams in particular, the physical environment is far from constant. Although there are many examples of strong species interactions in streams (Hildrew & Townsend, 1982; Hemphill & Cooper, 1983; MacAuliffe, 1984; Hart, 1987; Scrimgeour & Culp, 1994; Suhling, 1996; Kratz, 1996), it is generally assumed that harsh environments will limit the importance of biotic interactions (Peckarsky, 1983; Hansen *et al*, 1991; Lancaster, 1996).

In 1978 Connell proposed the Intermediate Disturbance Hypothesis to explain the high species diversity in rain forests and on coral reefs. He reasoned that there was a competitive hierarchy of species where, in the absence of disturbance, superior species would outcompete inferior ones, thus reducing species diversity. In this model when a disturbance occurs individuals are removed, opening up space for inferior competitors and thus increasing species richness. Under severe disturbance regimes, most individuals may be removed and species richness is low. Thus, highest diversity is to be expected at intermediate disturbances.

Huston (1979) independently developed the "dynamic equilibrium" model. He demonstrated that community structure could be determined by a 'balance' between species interactions and disturbance. Communities, through competitive

exclusion and predation, would move towards some final state. If disturbed, however, this process would be reset. If disturbance frequency was high, competitively inferior species would be able to persist, thus increasing species richness. Research supports the application of the dynamic equilibrium model to streams (eg Resh *et al*, 1988; Reice *et al*, 1988)

It is thus widely recognised that disturbance may play an important role in structuring stream communities (Pickett & White, 1985; Sousa, 1984; Resh *et al*, 1988; Townsend, 1989; Reice *et al*, 1990; Hildrew & Giller, 1994). Hildrew & Townsend (1987) and Townsend (1989) define disturbance as, "any relatively discrete event in time that removes organisms and opens up space or other resources that can be utilised by individuals of the same or different species".

In streams, one important source of disturbance is that due to high flows. Spates may directly increase the density-independent mortality of invertebrates (Niemi *et al*, 1990; Giller *et al*, 1991), although recent research suggests that high shear stress alone may not disturb individuals, unless it is associated with some degree of bed movement (Giberson & Cobb, 1995). It has long been recognised that uniform sediments of different particle sizes will begin to move at different velocities (Shields, 1936). Particle shape, the level of imbrication or interaction with surrounding particles and the size ranges of surrounding particles also contribute to the point of initial motion (e.g. Billi *et al*, 1992).

The frequency of disturbance is one way of describing the temporal heterogeneity of streams, and it provides a promising axis label for the Habitat Templet (Southwood, 1977, 1988), as discussed in Chapter 1. A suitable arbitrary measure of disturbance frequency is the number of days per year that a certain fraction of the stream-bed moves. For instance, Scarsbrook (1995) used the number of days that 50% of the bed moved as his measure of frequency of disturbance. Such measures are site-specific so, for the purposes of comparisons among sites, a

measure of the substratum particle sizes and the discharge required to move them is essential for each stream.

Granulometry provides such an estimate of the substratum particle size distribution in streams. It not only provides a general description of the bed sediments and their degree of sorting, but also yields estimates of the median particle size that can be used to calculate disturbance frequency. In this Chapter I present disturbance frequency data for all the sites sampled, and they will be used to generate one axis of a Habitat Templet.

3.2 Methods

3.2.i Substratum particle size distribution

At each of 23^{*} stream sites five replicate samples of 25 x 25 cm of bed substratum were removed from a riffle area. A Surber sampler was used to ensure that only the designated area was sampled, and to catch any small particles that would otherwise have been washed away. The top layer was sampled separately from the lower layer in order to determine the degree of armouring of the bed. The Surber sampler was placed on the stream bed, a visual assessment was made of the particle sizes, and the top layer within the Surber sampler was removed to a depth corresponding to the diameter of a median sized stone (as determined by the visual assessment). The sample was bagged and labelled. With the Surber sampler still in place, any sediment now exposed by the removal of the top layer was then removed to approximately the same depth as the top layer and bagged. Finally, when removing the Surber sampler, any sediment washed into the net was added to the bag containing the lower sediment layer.

In the laboratory the stones were washed through a series of sieves of decreasing mesh sizes, and each size class was dried in the oven at 60°C for two days. The stones were then weighed, and the cumulative weight as a percentage was

^{*} The 26 stream sites were reduced to 23 when Kidbrooke Park i & ii, Marden's Hill i & ii and Old Lodge i & ii were merged. These pairs of sites were close together (within tens of metres of each other) and were assumed to have identical habitat characteristics.

then plotted against the mesh size, expressed as the Phi number. The Phi number has traditionally been used in granulometry to express mesh sizes; it is a logarithmic transformation ($\log_{10} [\text{mesh mm}] / \log_{10} 2$).

3.2.ii. Substratum particle movement (tracer particles)

For each ^{of the 23 sites} stream, particles of the median and ± 25 percentile sizes were painted in five different fluorescent colours using standard gloss paint. There were 3-7 stones of each size class in each colour, so on average each colour-group contained 15 stones. Each particle was marked according to size for easy identification in the field.

At the ²³ field sites the stones were placed in five rows*, each row having a separate colour, and the position of the rows were marked in the stream banks by gardening sticks painted in the corresponding colour. Within each row, the stones were placed randomly to avoid bias, and after each measurement all stones were removed and replaced randomly, even if no movement occurred. This was to ensure that if a stone was sheltered behind a larger stone this would only affect that stone once.

The sites were then left for between a week and two months, depending on rainfall; during heavy rainfall the sites were visited more frequently than during periods of drought, thus sometimes the sites were visited twice in a week, while at other times up to two months would pass between visits. During each visit, any particle movement was recorded, and the distance moved measured. Movements less than 10 cm were regarded as no movement. This was done to allow for the natural settling of particles. The particles were then placed back in the appropriate rows randomly.

For each sampling occasion discharge was estimated. Velocity was recorded at three to five spots across the channel width using a "mini" bucket wheel

* The distance between rows varied between 0.5-1 m depending on the length of riffle section available.

† This method is bias towards very small particles such as silt or sand. Particle sizes as low as 1 mm diameter were measured, however, and, because sampling was carried out in riffle areas, small particle sizes are likely to make out only a small proportion of the total.

velocity meter (5 cm in diameter). The depth in three to five spots across the channel and the width were also recorded. This was repeated across two or three transects. Discharge was then calculated according to the formula:

$$\text{Discharge (m}^3\text{s}^{-1}\text{)} = [\text{mean depth (m)} * \text{width (m)}] * \text{mean velocity (ms}^{-1}\text{)}$$

3.2.iii. Substratum particle size and stability

In all 23 sites an alternative method of determining the substratum particle size and stability was used, based on Sear's (1992) modification of Wolman's (1954) method. In a riffle reach one hundred particles were picked at random by wading across the substratum from bank to bank and picking up the particle that was immediately below the big toe*. Each particle was measured along its three axes, and it was noted whether the particle was tight to remove or loose, and whether it was exposed or interacting with other particles.

The particle sizes, for comparison with the sieved samples in section 3.2.i, were determined from the median (b) axes of all particles. An estimate of substratum stability was obtained from the ratio of stable particles (tight or interacting) to unstable particles (loose or exposed).

3.3 Results

3.3.i Substratum particle size distribution

The majority of the streams investigated had very similar substrata. The 'Very Coarse Gravel Bed' streams (from now on called coarse gravel bed streams) had a median particle size ranging from about 35 mm (Cackle Street) to about 68 mm (Marden's Hill) (see Table 3.1 for a description of substratum particle sizes in the different stream categories). The 'Fine Gravel Bed' streams were Batt's Bridge (7.6 mm) and Weirwood Road (20 mm), and Boringwheel Mill is classed as a Coarse Gravel Bed stream and had a ^{broken} "slate-like" substratum with a median diameter of 25 mm (these three sites will from now on be called fine gravel bed streams).

Table 3.1. Grade scale for substratum particle size (after Brakensiek *et al*, 1979), for the sizes relevant to the streams investigated.

Class (Wentworth)	Particle diameter (mm)	ϕ
Very coarse gravel	32-64	-6 to -5
Coarse gravel	16-32	-5 to -4
Medium gravel	8-16	-4 to -3
Fine gravel	4-8	-3 to -2
Very fine gravel	2-4	-2 to -1

The results of the granulometry can be seen in Figs 3.1-3.3. In all but two streams (Withyham (Fig 3.1.h) and Boringwheel Mill (Fig 3.3.c)), the upper (armour) layer was sampled separately from the lower layer. The particles in Withyham were so large and varied that it was difficult to determine how deep the armour layer was, and whether smaller particles between the larger stones were part of the upper or the lower layer. Boringwheel Mill was fast flowing and so well armoured that, when the top particles were removed, the smaller lower particles were immediately washed into the same Surber. Both of these sites, therefore, were sampled without separating the upper and lower layers.

Most streams show a distinct separation in particle size between the upper and lower layers. This indicates 'armouring', the situation where the upper layer protects the lower layer from the forces of the flow. It occurs when fines are differentially entrained in the flow creating a superficial layer of particles, in contact with the flow, with a median size greater than that in the layer below. Armouring is typically associated with coarse gravel bed streams. Batt's Bridge (Fig 3.1.a) and Weirwood Road (Fig 3.3.e), both of which have relatively small median substratum

Figure 3.1. Substratum particle size distribution (Mean \pm SE, $n=5$, on ArcSine transformed values) for a) Batt's Bridge, b) Clockhouse Lane, c) Maresfield, d) Old Forge, e) Old Lodge, f) Below Friar's Gate, g) Withyham Green, h) Withyham
NB. Armour and lower layer were not distinguished at Withyham.

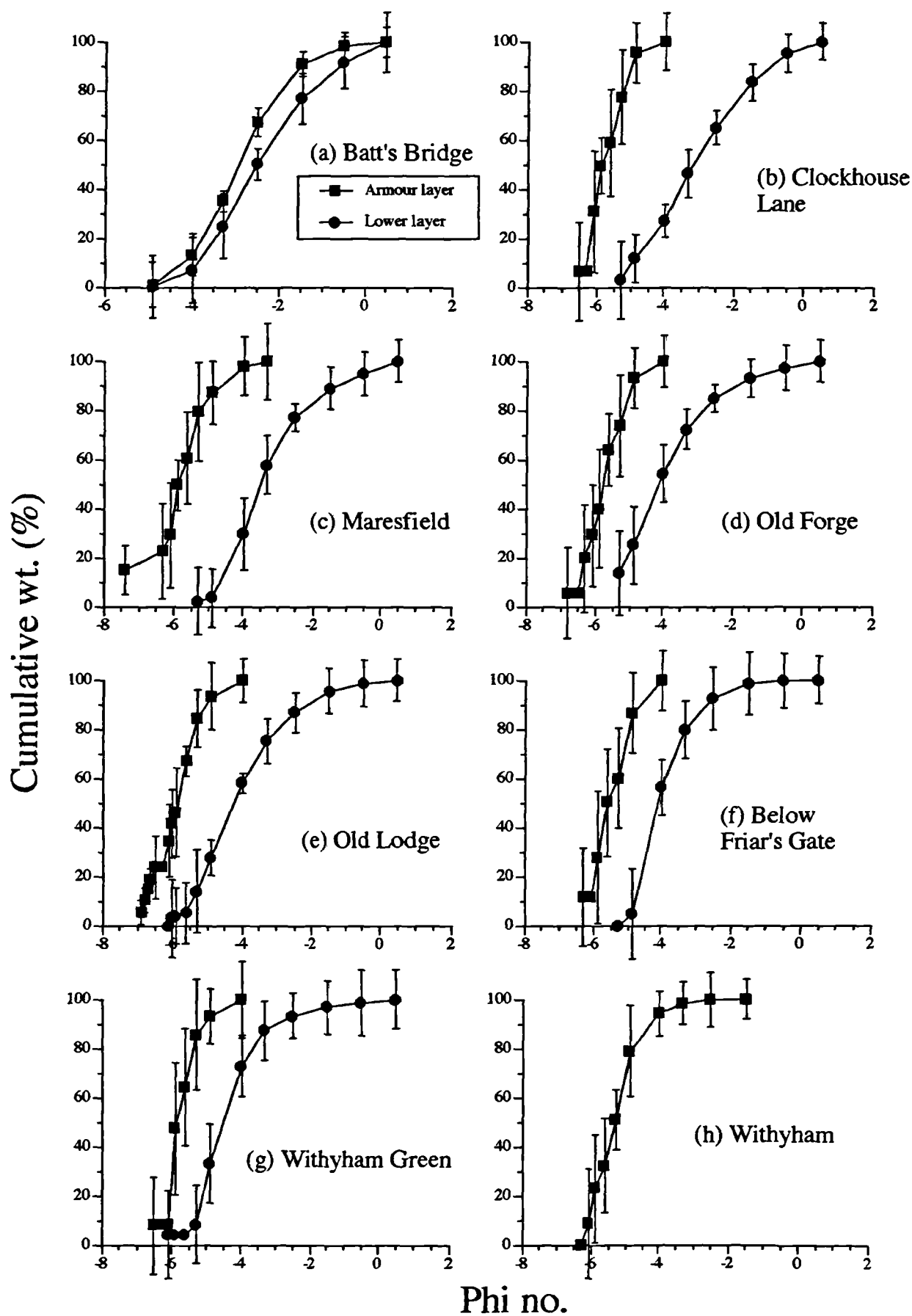


Figure 3.2. Substratum particle size distribution (Means \pm SE, $n=5$, on ArcSine transformed values) for a) Marden's Hill, b) Broadstone Stream, c) Dodd's Bottom, d) Marsh Green, e) Lone Oak, f) Hendall, g) Fairwarp, h) Cackle Street

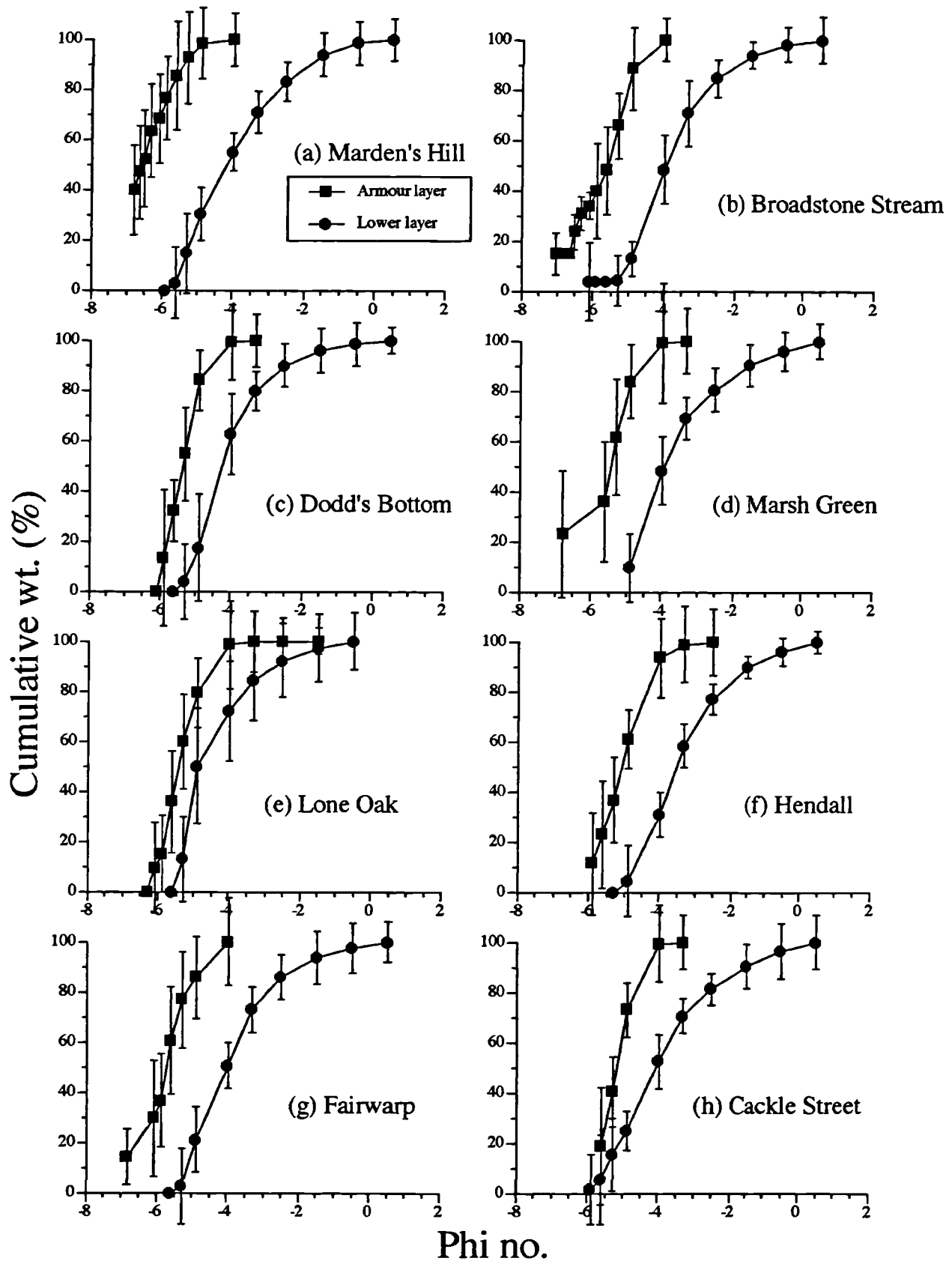
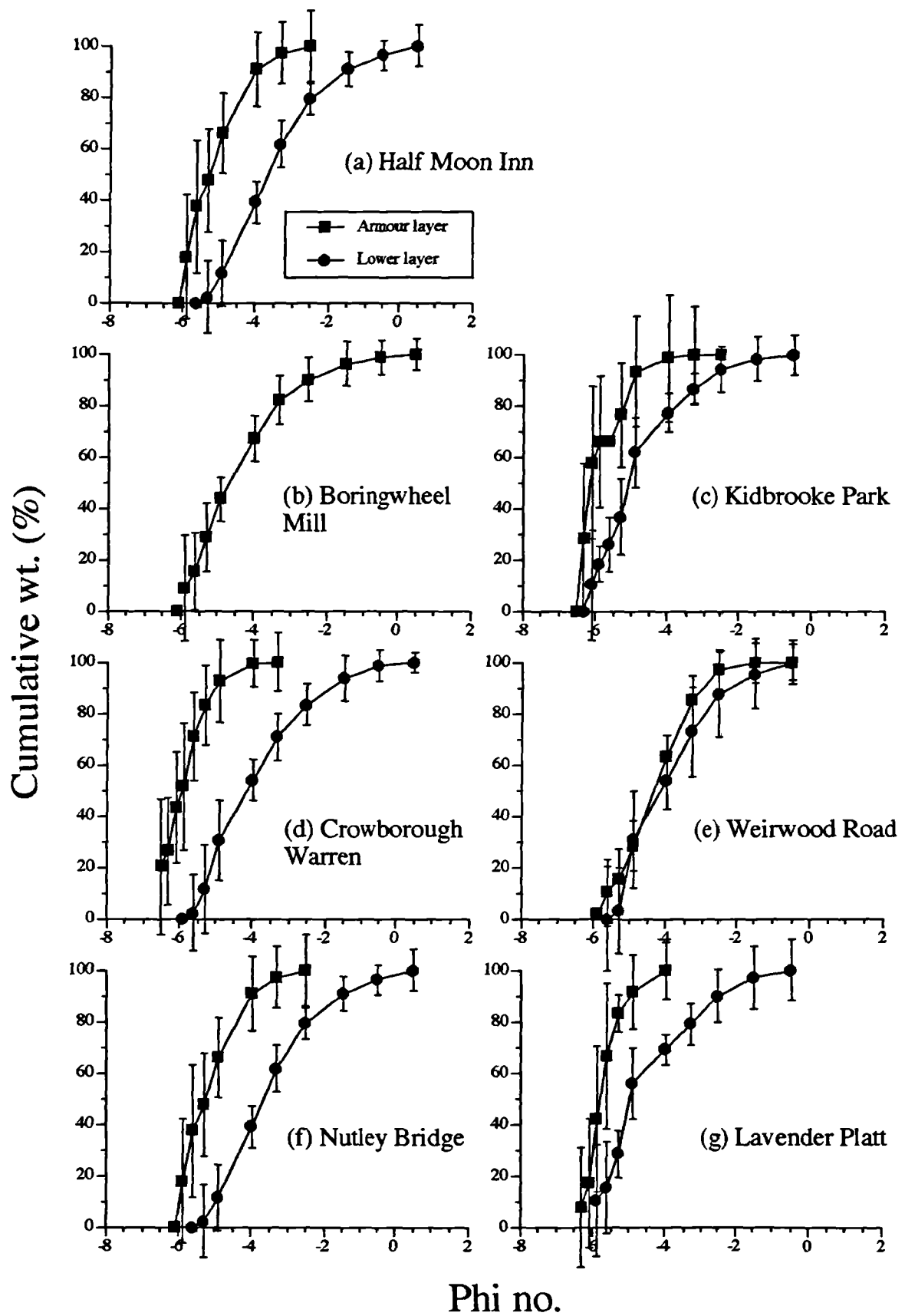


Figure 3.3. Substratum particle size distribution (Mean \pm SE, $n=5$, on ArcSine transformed values) for a) Half Moon Inn, b) Boringwheel Mill, c) Kidbrooke Park, d) Crowborough Warren, e) Weirwood Road, f) Nutley Bridge, g) Lavender Platt
NB. Armour and lower layer were not distinguished at Boringwheel Mill.



particle sizes (Table 3.2), are not armoured. Less distinct armouring was also found at Lone Oak and Kidbrooke Park (Figs 3.2.e & Fig 3.3.c). Well armoured streams are considered to be more stable than poorly armoured streams (Gurnell, pers. com.).

From the granulometry graphs the median and $\pm 25\%$ quartile sizes of the armour layers were determined (Table 3.2). Only the armour layers (or overall means where the armour layers were not sampled separately) were examined because the particles in these layers are the ones influenced by the flow.

The phi quartile skewness and deviation were calculated according to the formulae:

$$\text{Skewness: } Skq\phi = (Q3\phi + Q1\phi - 2Md\phi) / 2 \quad (\text{Krumbein, 1936})$$

$$\text{Deviation: } QD\phi = (Q3\phi - Q1\phi) / 2 \quad (\text{Briggs, 1977})$$

where $Q1\phi$ = the lower quartile phi number (25%), $Q3\phi$ = the upper quartile phi number (75%) and $Md\phi$ = the median phi number.

The phi quartile skewness indicates how equally or unequally the particles are sorted. This is basically an indication of the variation in grainsizes at either end of the size scale. For example, if large particles are sorted better than small, then there is a "tail" at the top of the graph, indicating a greater range in size amongst the small particles compared to the large particles.

If $Skq\phi = 0$, the small and large particles are sorted equally.

If $Skq\phi > 0$ the large particles are sorted better than the small, and

if $Skq\phi < 0$, the small particles are sorted better than the large. Most streams had a $Skq\phi$ of around 0 (Table 3.2). Withyham and Kidbrooke Park had high values, and Marsh Green a low value. From Figs 3.1.h & 3.3.d it can be seen that Withyham and Kidbrooke Park, respectively, have little variation in size amongst the large stones (steep curve), and a higher variation in the small size range (almost horizontal curve). Marsh Green (Fig 3.2.d) shows the opposite trend.

Table 3.2. Substratum particle size distribution (granulometry) for all sites arranged in order of increasing median particle size. Md ϕ = median phi no., Q1 ϕ = lower quartile phi no., Q3 ϕ = upper quartile phi no., Skq ϕ = phi quartile skewness, QD ϕ = phi quartile deviation. * indicates values of interest.

Site	Md ϕ	Median (mm)	Q1 ϕ	25% (mm)	Q3 ϕ	75% (mm)	Skq ϕ	QD ϕ
Batt's Bridge	-2.93	7.6	-3.66	12.6	-2.17	4.5	0.02	0.75
Weirwood Road	-4.30	19.7	-4.96	31.1	-3.83	14.2	-0.09	0.57
Boringwheel Mill	-4.64	24.9	-5.41	42.5	-3.64	12.5	0.11	0.89 *
Hendall	-5.06	33.4	-5.65	50.2	-4.43	21.6	0.02	0.61
Cackle street	-5.15	35.5	-5.53	46.2	-4.76	27.1	0.01	0.39
Nutley Bridge	-5.24	37.8	-5.72	52.7	-4.50	22.6	0.13	0.61
Dodd's Bottom	-5.33	40.2	-5.66	50.6	-5.05	33.1	-0.03	0.31
Withyham	-5.33	40.2	-5.83	56.9	-4.05	16.6	0.39 *	0.89 *
Lone Oak	-5.41	42.5	-5.80	55.7	-4.96	31.1	0.03	0.42
Half Moon Inn	-5.42	42.8	-5.76	54.2	-4.61	24.4	0.23	0.58
Marsh Green	-5.42	42.8	-6.58	95.7	-5.04	32.9	-0.39 *	0.77
Below Friar's Gate	-5.61	48.8	-5.87	58.5	-5.00	32.0	0.18	0.44
Broadstone Stream	-5.63	49.5	-6.50	90.5	-5.16	35.8	-0.20	0.67
Fairwarp	-5.63	49.5	-6.25	76.1	-5.30	39.4	-0.15	0.48
Old Forge	-5.73	53.1	-6.16	71.5	-5.24	37.8	0.03	0.46
Lavender Platt	-5.81	56.1	-6.07	67.2	-5.39	41.9	0.08	0.34
Clockhouse Lane	-5.85	57.7	-6.11	69.1	-5.30	39.4	0.15	0.41
Maresfield	-5.90	59.7	-6.29	78.2	-5.49	44.9	0.01	0.40
Old Lodge	-5.91	60.1	-6.25	76.1	-5.46	44.0	0.05	0.40
Withyham Green	-5.91	60.1	-6.08	67.6	-5.66	50.6	0.04	0.21
Crowborough	-5.92	60.5	-6.30	78.8	-5.53	46.2	0.00	0.39
Warren								
Kidbrooke Park	-6.08	67.6	-6.33	80.4	-5.03	32.6	0.40 *	0.65
Marden's Hill	-6.08	67.6	-6.50	90.5	-5.66	50.6	0.00	0.42

Positive skewness values, where large particles are better sorted than small, were found when there is a larger proportion of small substratum particles in the sample. This is true for Withyham, where no discrimination was made between upper and lower layers when sampling. Kidbrooke Park also had a positive skewness value. This stream had a less distinct armour layer (Fig 3.3.c) than most of the others, and it is a slow-flowing, relatively deep stream where small substratum particles do not easily get washed out of the upper layer. Marsh Green (Fig 3.2.d) is the only stream with a high negative skewness value. This is a fast flowing stream, with a high proportion of large particles compared to small.

Phi quartile deviation ($QD\phi$) indicates variation in particle sizes in general. If the value is high there is some variation, if it is low there is little or no variation in particle size. The streams can be divided into different classes (Gordon *et al*, 1992):

< 0.35	very low variation
0.35 - 0.50	low variation
0.50 - 1.00	moderate variation
1.00 - 2.00	high variation
> 2.00	very high variation

In general, there was little difference in Phi Quartile Deviations between sites. Boringwheel Mill and Withyham showed the highest deviations (Table 3.2), although they are grouped in the same class as most other streams. These are the sites where no distinction was made in sampling between upper and lower layers. Generally most streams show low to moderate variation, and a few very low variation.

3.3.ii. Discharge

The Environment Agency, and previously the National Rivers Authority, maintains a gauging weir at Broadstone Stream. This measures the discharge once a

day every day of the year. However, the gauge broke down in 1994, and it remained unreliable in 1995. It was possible, however, to relate the 1993 Broadstone gauge data to the data from another gauge maintained by the Environment Agency at Chafford. Chafford lies about 10 kilometres downstream of Broadstone Stream and is on the River Medway. Although discharge was much higher at this station, the regression was highly significant ($p < 0.001$) (Fig. 3.4). Using this relationship between the gauged discharge at Broadstone and Chafford for 1993, and gauged discharges at Chafford in 1994-95 (the period of my substratum movement experiments), a discharge record for Broadstone was estimated for 1994-95.

Individual spot discharge measurements made at the time of the experiments in Broadstone Stream were then correlated to the 'recreated' measurements at Broadstone Stream (Fig. 3.5). The fit proved to be highly significant ($p < 0.001$). Spot discharge measurements for all the other streams were similarly correlated to the recreated Broadstone Stream record and were found to be significant (Table 3.3). An annual discharge hydrograph could thus be created for all streams. The Broadstone hydrograph from the recreated data is shown in Fig. 3.6.

Fig. 3.4. Regression analysis of (y) Broadstone discharge data against (x) Chafford discharge data. Both were measured at gauges in 1993 ($F = 752.80$, $p < 0.001$).

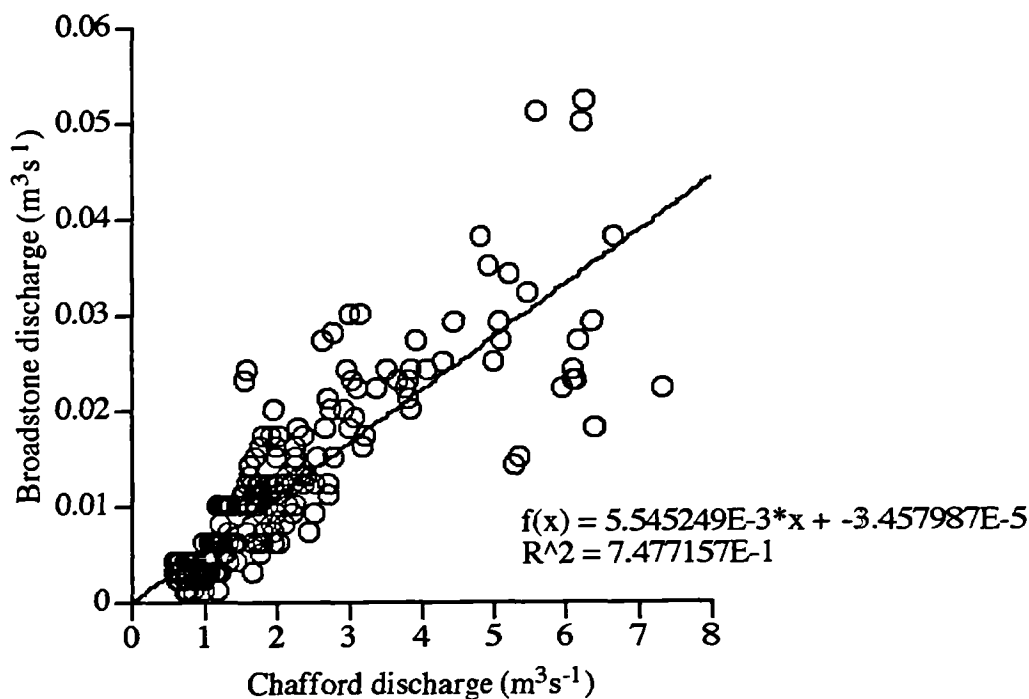
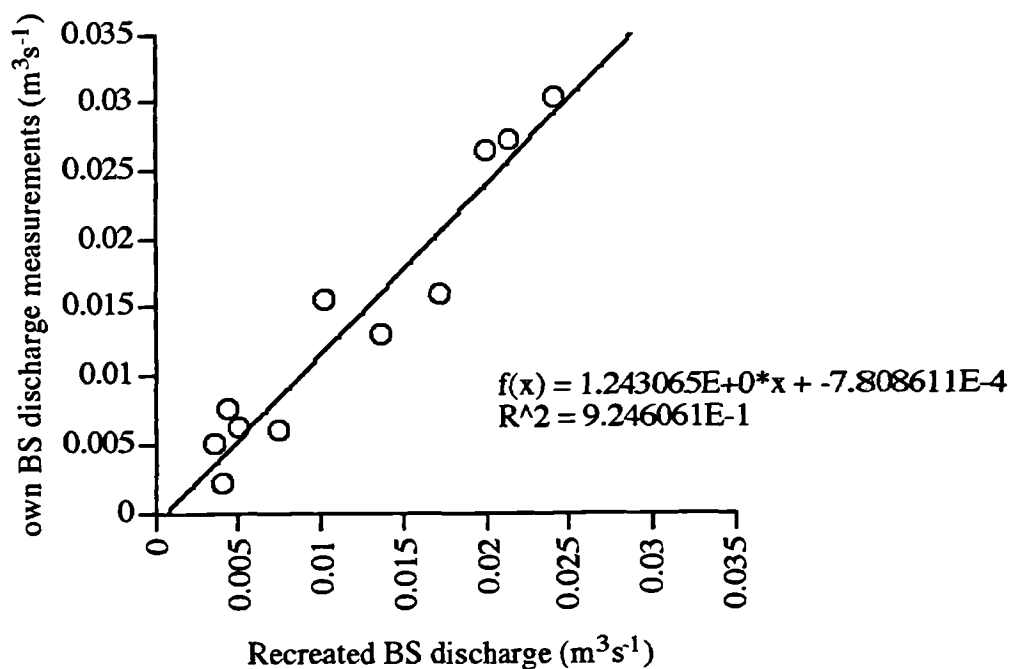


Fig. 3.5. Broadstone Stream. Regression of own discharge measurements against recreated discharge ($F = 108.71$, $p < 0.001$).



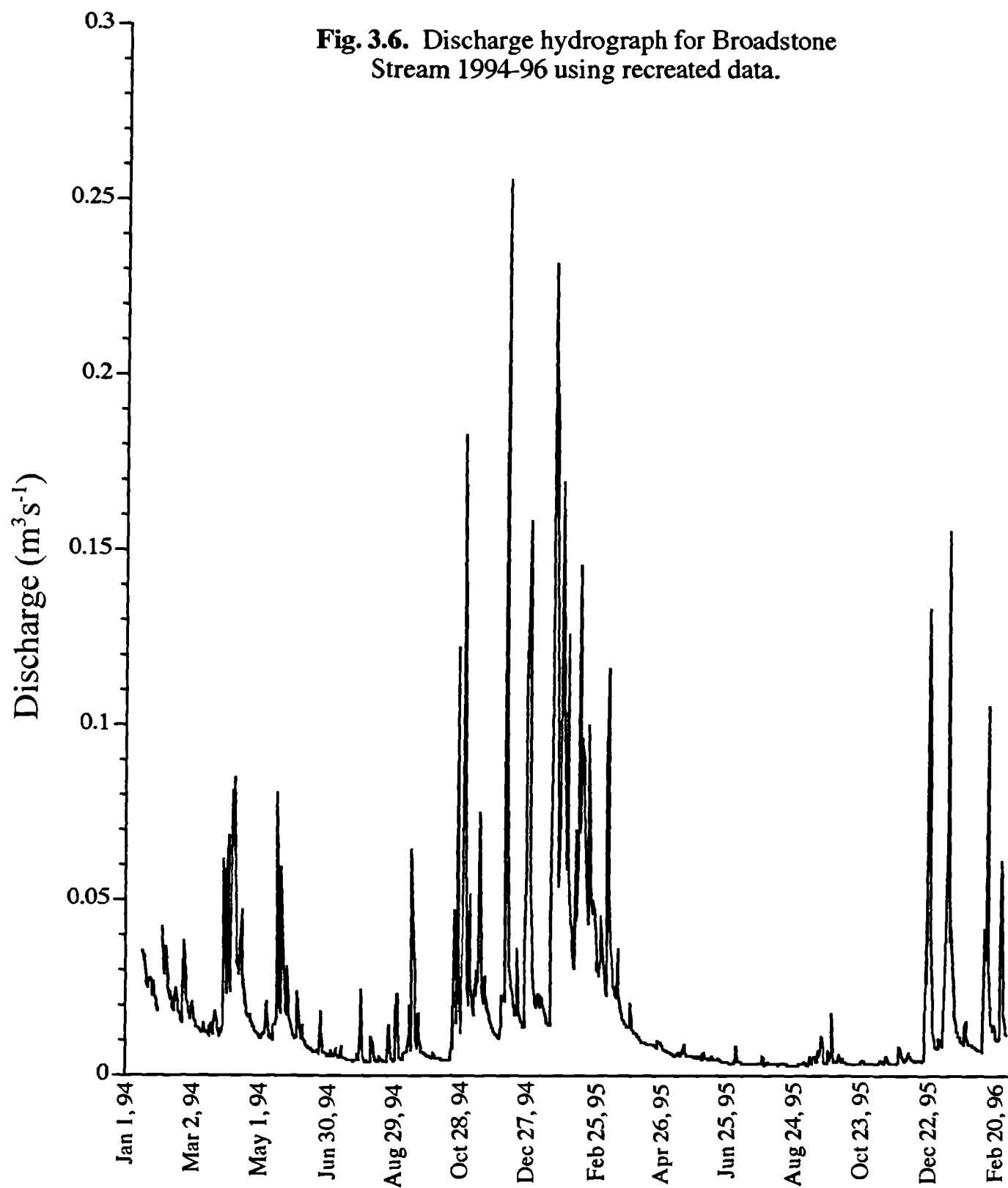


Table 3.3. Regression equations and goodness of fit statistics for (y) own discharge measurements, and (x) Broadstone calculated discharge at all sites.
 $p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***, ns = not significant.

SITE	REGRESSION EQUATIONS	F	P
Lavender Platt	$y = 0.8046x + 0.0019$	65.14	***
Weirwood Road	$y = 1.4544x - 0.0019$	263.31	***
Kidbrooke Park	$y = 2.0656x - 0.0048$	54.68	***
Nutley Bridge	$y = 4.7256x + 0.0027$	26.31	**
Old Lodge	$y = 5.5712x - 0.0408$	340.31	***
Lone Oak	$y = 0.8332x + 0.0081$	13.29	**
Crowborough Warren	$y = 1.0384x - 0.0071$	34.41	**
Cackle Street	$y = 0.7736x + 0.0121$	25.55	***
Dodd's Bottom	$y = 1.8288x + 0.0109$	141.89	***
Fairwarp	$y = 4.6602x + 0.0138$	227.46	***
Marden's Hill	$y = 7.5408x - 0.0178$	149.35	***
Below Friars Gate	$y = 7.4721x + 0.0024$	113.2663	***
Old Forge	$y = 8.6190x - 0.0039$	111.70	***
Batt's Bridge	$y = 9.4400x + 0.0330$	16.28	**
Maresfield	$y = 11.7964x - 0.0176$	170.34	*
Marsh Green	$y = 10.6007x + 0.1079$	36.06	***
Half Moon Inn	$y = 9.8285x + 0.0288$	62.8293	***
Withyham	$y = 13.5940x + 0.0429$	31.76	**
Clockhouse Lane	$y = 2.1652x + 0.0090$	8.05	*
Withyham Green	$y = 18.4579x - 0.0322$	231.31	***
Boringwheel Mill	$y = 6.2414x - 0.0032$	108.73	***
Broadstone Stream	$y = 1.2405x - 0.0008$	108.712	***

3.3.iii. Substratum particle movement

The point of initial motion of the substratum is likely to be more important to the benthic organisms than the distance those particles travel along the stream bed. The distance particles travelled was measured and proved to be significantly correlated with discharge in most streams, and any differences in distance particles travelled between streams might simply reflect differences in discharge. In order to ~~eliminate~~ the effects of the range of discharges found amongst the streams investigated, it was important to use a unitless measure of particle movement, so the percent movement of stones of each size was calculated at each stream.

An Analysis of Covariance (ANCOVA) showed that there was no significant difference between the percent movement of different stone sizes for any of the

streams at any discharge (Table 3.4 & Fig. 3.7). Percent stone movement did vary with discharge, however, in all but two streams: Withyham Green and Weirwood Road. At Withyham Green frequent human interference caused the total number of marked stones to be drastically reduced, throwing doubt on the analyses. At Weirwood Road a fallen tree and subsequent log jam caused a dam to be formed halfway through the experiment, which drastically altered the flow of the stream and therefore the movement of the particles.

A common regression of all stones combined against discharge for each site proved highly significant except for these two artificially disturbed sites (Table 3.5). An inverse regression (Table 3.6) then enabled a calculation of the discharge required to move 50% of the stones in each stream. This was then related to the discharge hydrographs for each stream to calculate how often this was equalled or exceeded in a year (Table 3.7).

* Maresfield and Hendall were excluded from the experiment at this stage. Hendall was difficult to access and did not have suitable riffle sections to study. In Maresfield particles were either removed by frequent human intervention or particles were blackened by biofilm so rapidly that they were difficult to recover. Consequently only 21 stream sites were included in this analysis.

Table 3.4. Analysis of covariance (ANCOVA) and goodness of fit statistics for percent substratum movement against stone sizes with discharge as covariable at 21 sites.
 $p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***, ns = not significant.

SOURCE	SS	df	MS	F	P
Lavender Platt					
Stone size	84.5267	2	42.2633	0.07	ns
Discharge	15908.5072	1	15908.5072	26.42	***
Weirwood Road					
Stone size	550.8752	2	275.4376	0.59	ns
Discharge	1595.5265	1	1595.5265	3.41	ns
Kidbrooke Park					
Stone size	92.6973	2	46.3487	0.84	ns
Discharge	10907.6461	1	10907.6461	198.69	***
Nutley Bridge					
Stone size	133.2013	2	66.6007	2.26	ns
Discharge	11067.8174	1	11067.8174	375.78	***
Old Lodge					
Stone size	46.9817	2	23.4908	0.04	ns
Discharge	6740.7320	1	6740.7320	14.24	**
Lone Oak					
Stone size	100.7660	2	50.3830	0.16	ns
Discharge	30297.6510	1	30297.6510	98.13	***
Crowborough Warren					
Stone size	662.0400	2	331.0200	0.76	ns
Discharge	13593.2528	1	13593.2528	31.56	***
Cackle Street					
Stone size	187.4408	2	93.7204	0.15	ns
Discharge	23017.5481	1	23017.5481	39.21	***
Dodd's Bottom					
Stone size	662.6252	2	331.3126	0.80	ns
Discharge	9275.8113	1	9275.8113	22.54	***
Fairwarp					
Stone size	351.8178	2	175.9089	0.45	ns
Discharge	14446.8415	1	14446.8415	37.20	***
Marden's Hill					
Stone size	58.3457	2	29.1729	0.07	ns
Discharge	8222.6048	1	8222.6048	21.87	***
Below Friars Gate					
Stone size	35.2011	2	17.6006	0.15	ns
Discharge	27526.2507	1	27526.2507	246.14	***
Old Forge					
Stone size	146.9078	2	73.4539	0.13	ns
Discharge	4889.9696	1	4889.9696	8.68	*
Batt's Bridge					
Stone size	9.6929	2	4.8465	0.007	ns
Discharge	13479.3655	1	13479.3655	19.76	***

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(Table 3.4. continued from previous page)

SOURCE	SS	df	MS	F	P
Marsh Green					
Stone size	120.3758	2	60.1879	0.11	ns
Discharge	25525.1148	1	25525.1148	49.52	***
Half Moon Inn					
Stone size	129.2410	2	64.6205	0.12	ns
Discharge	8852.9195	1	8852.9195	17.11	***
Withyham					
Stone size	158.7629	2	79.3814	0.10	ns
Discharge	7331.2104	1	7331.2104	9.43	**
Clockhouse Lane					
Stone size	218.2300	2	109.1150	0.30	ns
Discharge	29536.2423	1	29536.2423	82.83	***
Withyham Green					
Stone size	1316.1638	2	658.0819	0.97	ns
Discharge	9.4411	1	9.4411	0.01	ns
Boringwheel Mill					
Stone size	274.6695	2	137.3348	1.01	ns
Discharge	1816.3652	1	1816.3652	13.48	**
Broadstone Stream					
Stone size	506.7387	2	253.3693	0.58	ns
Discharge	11455.3058	1	11455.3058	26.52	***

Fig. 3.7. Regression of percentage substratum particle movement against discharge for all sites and all particle sizes.

% substratum particle movement

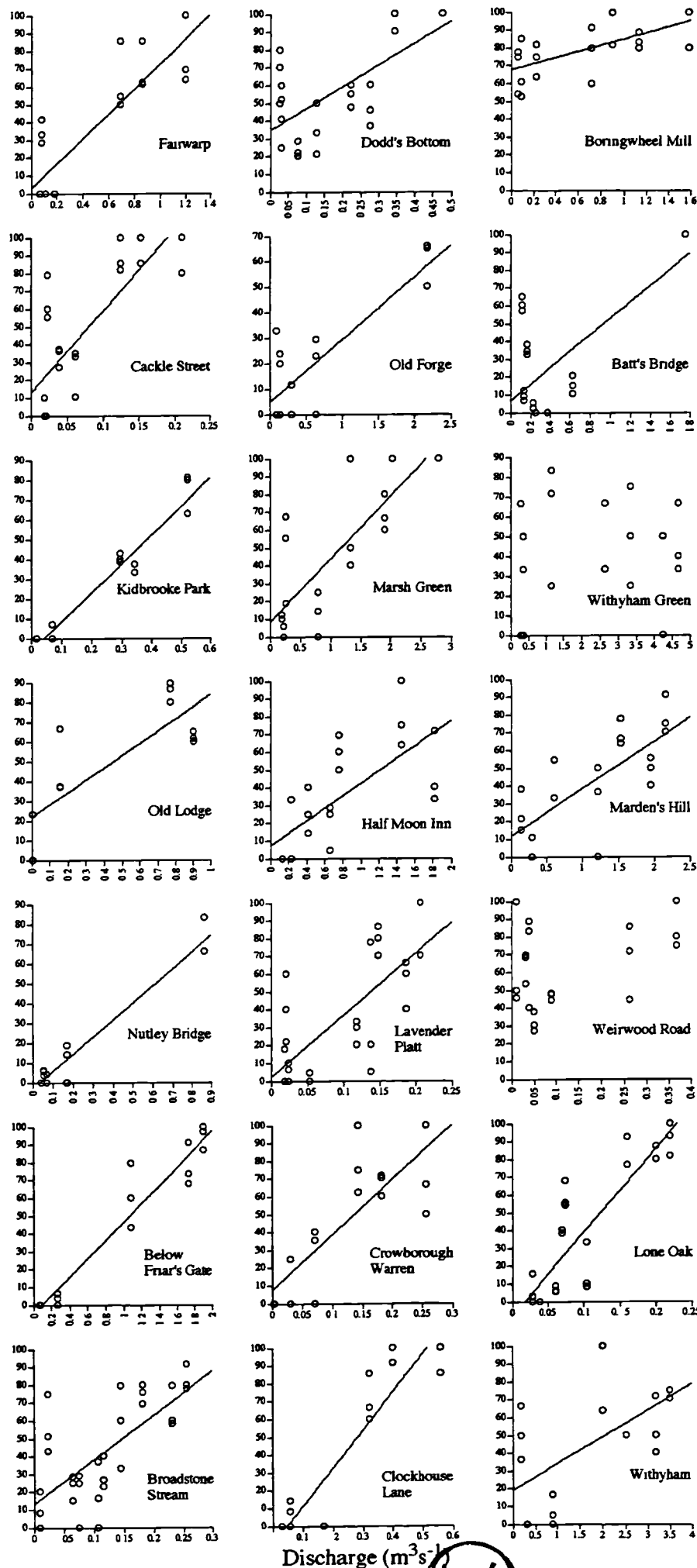


Table 3.5. Regression equations and goodness of fit statistics for (y) percent substratum movement, and (x) discharge at all sites for all stone sizes combined.
 $p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***, ns = not significant.

SITE	REGRESSION EQUATIONS	F	P
Lavender Platt	$y = 346.2840x + 2.3963$	28.5506	***
Weirwood Road	$y = 68.1622x + 53.1406$	3.5736	ns
Kidbrooke Park	$y = 145.2855x - 5.9003$	203.5759	***
Nutley Bridge	$y = 86.0030x - 2.9109$	314.7155	***
Old Lodge	$y = 61.8786x + 22.0749$	17.5930	**
Lone Oak	$y = 471.0188x - 7.9568$	104.3730	***
Crowborough Warren	$y = 309.5935x + 7.9005$	32.5007	***
Cackle Street	$y = 458.1623x + 13.4104$	42.4545	***
Dodd's Bottom	$y = 121.8891x + 34.8961$	22.9033	***
Fairwarp	$y = 66.4826x + 6.1969$	39.9354	***
Marden's Hill	$y = 26.7817x + 11.8070$	24.2223	***
Below Friars Gate	$y = 51.2297x - 4.5809$	275.1194	***
Old Forge	$y = 22.9707x + 13.6433$	9.7441	**
Batt's Bridge	$y = 45.9751x + 6.9999$	21.7251	***
Marsh Green	$y = 35.2623x + 8.6258$	53.8462	***
Half Moon Inn	$y = 34.9620x + 7.5516$	18.8541	***
Withyham	$y = 14.9044x + 19.2544$	10.4237	**
Clockhouse Lane	$y = 213.5277x - 10.0446$	90.7038	***
Withyham Green	$y = 0.3992x + 44.3980$	0.0140	ns
Boringwheel Mill	$y = 17.2878x + 67.9096$	13.4595	**
Broadstone Stream	$y = 248.7608x + 13.4534$	27.3278	***

Table 3.6. Inverse regression equations and goodness of fit statistics for (y) discharge, and (x) percent substratum movement at all sites for all stone sizes combined.

p < 0.05 *, p < 0.01 **, p < 0.001 ***, ns = not significant.

SITE	INVERSE REGRESSION EQUATIONS	F	P
Lavender Platt	$y = 0.0015x + 0.0440$	28.5506	***
Weirwood Road			ns
Kidbrooke Park	$y = 0.0065x + 0.0532$	203.5759	***
Nutley Bridge	$y = 0.0112x + 0.0421$	314.7155	***
Old Lodge	$y = 0.0103x - 0.0609$	17.5930	**
Lone Oak	$y = 0.0017x + 0.0342$	104.3730	***
Crowborough Warren	$y = 0.0022x + 0.0207$	32.5007	***
Cackle Street	$y = 0.0014x + 0.0085$	42.4545	***
Dodd's Bottom	$y = 0.0039x - 0.0433$	22.9033	***
Fairwarp	$y = 0.0107x + 0.0826$	39.9354	***
Marden's Hill	$y = 0.0209x + 0.2488$	24.2223	***
Below Friars Gate	$y = 0.0184x + 0.1316$	275.1194	***
Old Forge	$y = 0.0165x + 0.1809$	9.7441	**
Batt's Bridge	$y = 0.0108x + 0.1545$	21.7251	***
Marsh Green	$y = 0.0201x + 0.1730$	53.8462	***
Half Moon Inn	$y = 0.0142x + 0.2849$	18.8541	***
Withyham	$y = 0.0238x + 0.7092$	10.4237	**
Clockhouse Lane	$y = 0.0040x + 0.0787$	90.7038	***
Withyham Green			ns
Boringwheel Mill	$y = 0.0240x - 1.2343$	13.4595	**
Broadstone Stream	$y = 0.0020x + 0.0346$	27.3278	***

Table 3.7. Summary of disturbance frequencies for 21 streams measured in days per year.

SITE	DISTURBANCE FREQUENCIES (DAYS PER YEAR)	PROPORTION	PERCENTAGE (%)
Weirwood Road	N/A		
Withyham Green	N/A		
Kidbrooke Park	3	0.00821	0.821
Marden's Hill	5	0.0136	1.36
Lavender Platt	9	0.0246	2.46
Lone Oak	10	0.0273	2.73
Crowborough Warren	10	0.0273	2.73
Below Friars Gate	10	0.0273	2.73
Withyham	10	0.0273	2.73
Nutley Bridge	12	0.0328	3.28
Fairwarp	12	0.0328	3.28
Clockhouse Lane	13	0.0356	3.56
Old Forge	14	0.0383	3.83
Broadstone Stream	16	0.0438	4.38
Marsh Green	18	0.0493	4.93
Half Moon Inn	20	0.0547	5.47
Old Lodge	24	0.0657	6.57
Cackle Street	26	0.0712	7.12
Dodd's Bottom	26	0.0712	7.12
Batt's Bridge	30	0.0821	8.21
Boringwheel Mill	365	1.0000	100

Batt's Bridge was found to be disturbed 30 days per year, and Boringwheel Mill according to the these analyses was disturbed every day of the year.* Batt's Bridge has a very fine substratum, and Boringwheel Mill is the site with the slate-like substratum. Weirwood Road, the other fine gravel bed stream could not be determined because the regression was not significant. All other sites are coarse gravel bed streams; they had disturbance frequencies between 3 days per year (Kidbrooke Park) and 26 days per year (Cackle Street and Dodd's Bottom).

*

The regression for Boringwheel Mill on page 49 (Fig. 3.7) shows 50% of the substratum to be in movement at zero discharge, i.e. this site is disturbed 365 days per year according to the tracer particle experiment. This result will be analysed in the discussion.

3.3.iv. Substratum particle size and stability (Wolman method)

The substratum sizes derived from this method were generally well related to the estimates created by the sieving method, although the exact estimates differed (Table 3.8 & Fig. 3.8). Wolman's estimates were slightly lower than sieving estimates.

The stability estimates in general ranked the streams in the same order as the disturbance frequencies calculated from the particle movement (Fig. 3.9). The major exceptions are Boringwheel Mill, Dodd's Bottom and Marden's Hill.

Table 3.8. Substratum particle sizes (mm); comparing results from granulometry and from Wolman's method.

SITE	25% 'Wolman'	25% sieve	Median 'Wolman'	Median sieve	75% 'Wolman'	75% sieve
Weirwood Road	10	14	15	19	22	31
Kidbrooke Park	19	33	34	68	58	80
Nutley Bridge	16	22	32	37	45	52
Old Lodge	20	44	32	60	49	76
Lone Oak	25	31	55	42	90	56
Crowborough Warren	27	46	42	60	69	79
Cackle Street	20	27	32	35	48	46
Dodd's Bottom	17	33	34	40	52	51
Fairwarp	20	39	31	49	45	76
Marden's Hill	28	51	48	68	78	90
Old Forge	26	38	41	53	69	72
Marsh Green	26	33	39	43	53	96
Withyham	27	51	36	60	54	68
Clockhouse Lane	23	40	39	58	62	69
Boringwheel Mill	20	12	28	25	37	42
Broadstone Stream	16	35	29	49	48	90

Fig. 3.8. A comparison of substratum particle sizes obtained by using Wolman's and sieve methods. a) The median and ± 25 percentile particle sizes are plotted separately. The line shows the situation where the two methods give exactly the same result. b) All sizes are considered together, and a regression line is fitted.

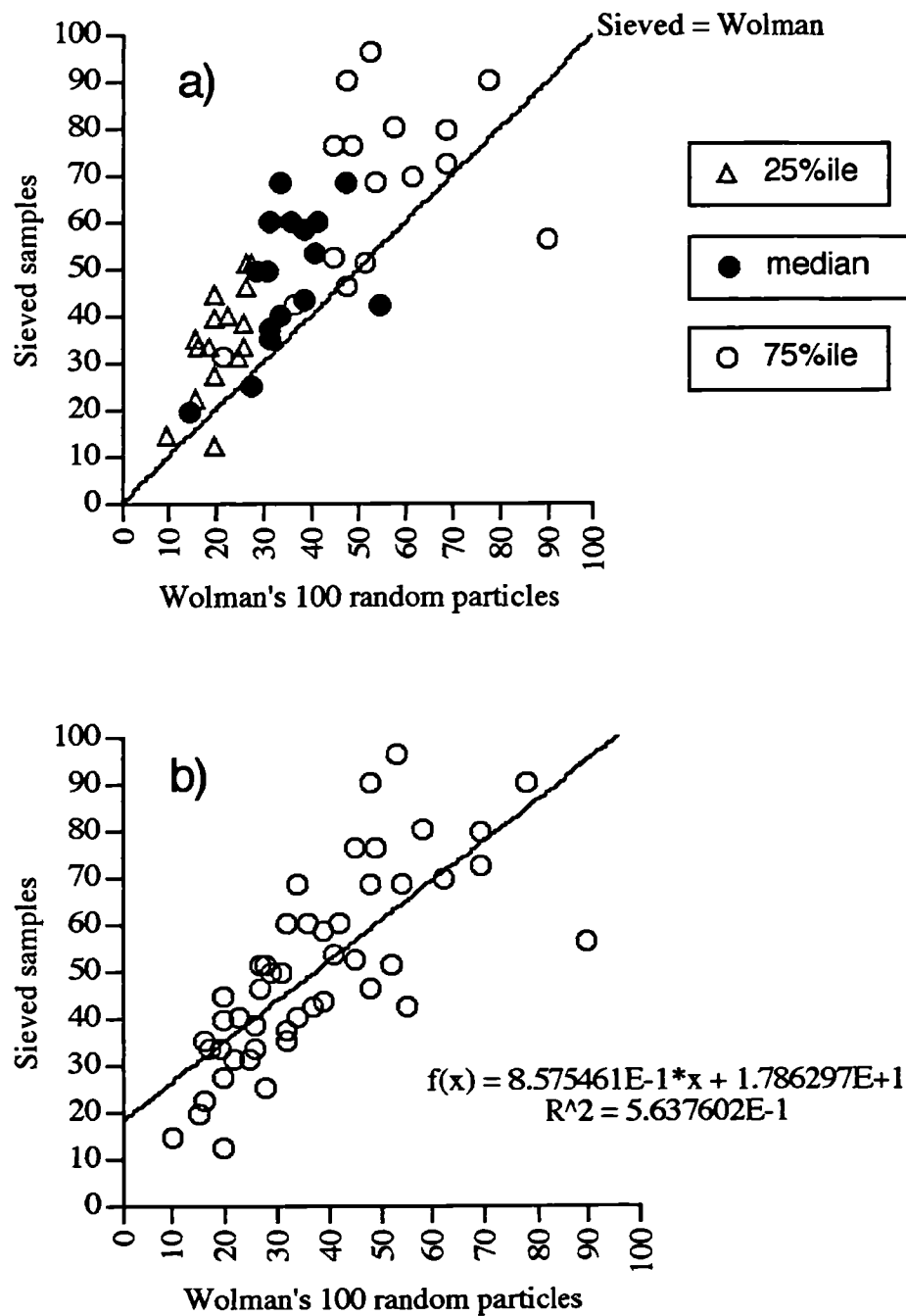
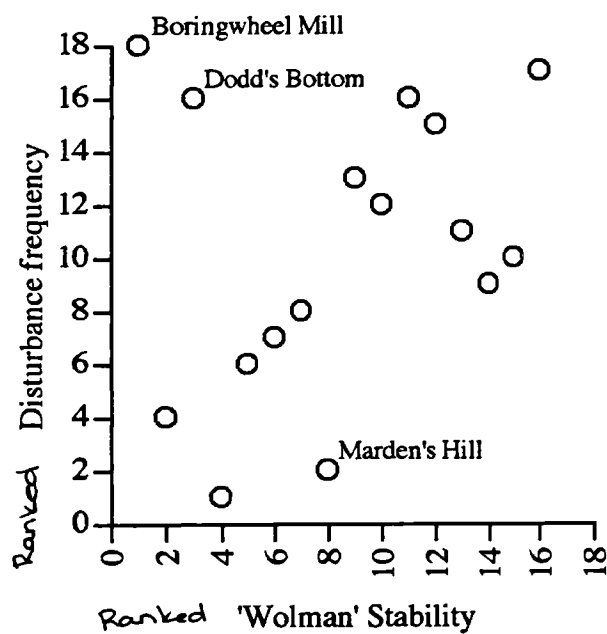


Fig. 3.9. A comparison of sites as ranked by decreasing bed stability using Wolman's method and increasing disturbance frequency using tracer particles.



3.4 Discussion

3.4.i. Coarse gravel bed streams compared to others

A distinction can be made between the coarse and fine gravel bed streams (Batt's Bridge and Boringwheel Mill). In general, the coarse gravel bed streams were less frequently disturbed, they had a larger median substratum particle size and were all very well armoured.

Batt's Bridge had a smaller substratum particle size and very poor armouring. Both the particle movement and Wolman's method showed this stream to have a high disturbance frequency. Unfortunately the other stream with small median substratum particle diameter, Weirwood Road, drastically changed flow during the experiment due to the appearance of a dam and showed no statistically significant relationship between substratum movement and discharge, so this stream could not be used for comparison.

Boringwheel Mill had 50% of the painted particles in motion at even the lowest measured discharge, so the disturbance frequency for this stream was set at 365 days per year. Wolman's measure of stability at Boringwheel Mill was very high, however, because most particles were interacting (Fig. 3.9). This result highlights the problems and advantages with each method; painted particles measure the actual movement of particles in relation to discharge, but the particles are positioned on the stream bed artificially. Wolman's method assesses the natural position of particles in relation to others, but does not predict the point of entrainment. Observations suggest that the stream bed is very stable, as predicted by Wolman. When some bed movement starts at a high discharge or by physical disturbance caused by humans or other animals, the armouring is broken, causing large areas ^(several metres) of stream bed to go into motion. A further complication is added, when considering the species inhabiting the stream; there is a very large population of *Hydropsyche* sp. at Boringwheel Mill. This net-spinning caddisfly binds the

substratum together with silken threads, actually adding to the stability of the stream bed. It is clear that to predict the disturbance frequency for Boringwheel Mill neither method provides the 'correct' answer. It is clear that the flow and bed movement in this site is unique among the sites investigated, so in subsequent analyses comparisons will be made where this site is included or left out. Due to the very high bottom shear stress measured in the stretch used for the tracer particles (Chapter 4), it is estimated that the disturbance frequency is higher than that found in any of the other sites, so therefore the disturbance frequency estimated by the tracer particles is used where the site is included in the analyses.

3.4.ii. Differences among coarse gravel bed streams

The differences among the coarse gravel bed sites were less. The two sites with the largest median substratum particle sizes, Kidbrooke Park and Marden's Hill were also the least frequently disturbed, but that was the only relationship found between substratum particle size and disturbance frequency amongst the coarse gravel bed streams. The differences with regards to armouring were negligible. There is a good deal of variation in disturbance frequencies between the coarse gravel bed streams, however, with values ranging from 3 (Kidbrooke Park) to 26 (Cackle Street & Dodd's Bottom) days per year. These differences may be explained by a complex interaction of physical factors such as the forces of flow, bed microtopography, particle shape, level of imbrication and turbulence to name but a few.

3.4.iii. Wolman's method as a predictor of substratum particle size and stability

Wolman's particle size estimates related well to those found using the sieving, although in general the values were slightly lower (Fig. 3.8). This difference may be explained by two factors (Sear, pers. com.); the first is that the sieve

estimates were made from particles collected in the armour layer. When the samples were collected, although much care was taken that the whole layer was removed, there will be a bias against the smaller particles. Wolman's method is less biased in this way. Secondly, Surbers were placed in the middle of the riffles when collecting samples for sieving, whereas the 100 random particles were collected by wading from bank to bank. This way particles closer to the edge were also sampled. The combination of these two factors may explain the trend towards a smaller predicted median substratum particle size using Wolman's method.

Wolman's stability estimates and the tracer particle estimates of disturbance frequency generally ranked the streams similarly. The major exceptions are Boringwheel Mill (discussed above), Marden's Hill and Dodd's Bottom. Marden's Hill had the largest substratum particle size of all the streams sampled (Table 3.2). Apart from the greater weight of these particles, substrata made up of large particles also have large interstitial spaces or 'pockets', where particles can more easily be detained (Sear, pers. com.), contributing to bed stability. Marden's Hill is therefore likely to be more stable than Wolman's method would indicate.

At Dodd's Bottom a small debris dam was present just upstream from the tracer particles when the experiment was started, and it was removed during a high flow event, thus changing the flow pattern affecting the particles during the experiment. In this case the stability predicted by Wolman may be more correct, as it is based on a point measure not affected by changes in flow patterns. The 100 random particles were measured upstream of where the dam had been.

In general Wolman's method produces estimates that relate well to those obtained by tracer particles and sieving. The main advantage of using Wolman's method is the speed and ease with which results can be obtained. Both the sieving and the tracer particle experiments were very time consuming, and the tracer particle movements were also dependent on precipitation. As well as the time factor, when

choosing either method, it must be considered whether initial motion or natural positioning of particles on the stream bed are more important in individual experiments. For the purpose of this thesis the disturbance frequencies estimated by the tracer particle movements will be used, as initial motion is likely to reflect the disturbance acting on benthic invertebrates more closely than does bed stability.

CHAPTER 4: Shear stress distributions and refugium availability.

4.1 Introduction

The potential importance of disturbance as a structuring force in communities is clear (Chapter 3). Stream communities are, however, surprisingly persistent (Hildrew & Giller, 1994; Milner, 1994). This suggests that the effect of disturbances may be ameliorated through the use of refugia. Robertson *et al* (1995) and Lancaster & Belyea (1997) highlighted the confusion there has been in the literature about the term 'refugia', and attempted to clarify its use. The first division they make concerns the spatial and temporal scale at which refugia may operate, and is usually related to the life span of the organisms in question (Hildrew & Giller, 1994). Thus, over time-periods greater than a generation time, refugia types include 'complex life cycles' and 'between-habitat' refugia (Lancaster & Belyea, 1997). Examples of these are the terrestrial adult life stages of insects or tributaries that are unaffected by the disturbance event.

Smaller-scale refugia (shorter than a generation time) also include both morphological/behavioural and physical refugium types. Lancaster & Belyea (1997) suggested 'changes in habitude' (changes in habits of individuals that render them less susceptible to disturbance), and 'within-habitat' refugia which refer to spatial and temporal heterogeneity. This thesis concentrates on this last type of refugium.

Spates sometimes result in severe population losses (Niemi *et al*, 1990; Giller *et al*, 1991; Flecker & Faifarek, 1994) but recolonisation is often rapid (Badri *et al*, 1987; Scrimgeour *et al*, 1988; Milner, 1994). This short-term disturbance and subsequent recovery suggests the presence of within-habitat refugia; areas where invertebrates may take refuge during high flow events, thus avoiding being washed away and enabling rapid colonisation after the event. The presence of instream flow refugia is now recognised (e.g. Lancaster & Hildrew, 1993; Palmer *et al*, 1995;

Robertson *et al.*, 1995), and their role in structuring communities has been postulated (Townsend, 1989; Hildrew & Giller, 1994; Hildrew, *in press*).

Several types of within-habitat refugia have been described; a downward migration into the hyporheic zone (Poole & Stewart, 1976; Marmonier & Creuzé des Châtelliers, 1991), lateral movements onto the flood plain (Schlosser, 1991), and instream flow refugia created by a spatially heterogeneous hydraulic environment (Townsend & Hildrew, 1994). This last type of refugium may be especially important in streams lacking either an extensive hyporheic zone or a flood plain.

Instream flow refugia can be described as areas that retain low hydraulic stress even at high discharge. They may be used actively or passively by stream communities. These areas may typically be associated with turbulent eddies, stream margins, wakes around roughness elements (e.g. tree roots or rocks), and reverse flows associated with pools and bends. These hydraulic "Dead Zones" can be quantified using transient storage models. The Aggregated Dead Zone model of Beer & Young (1983) calculates, over a stream reach, that fraction of water that is actively flowing and that which is stored in "Dead Zones" (measured as the Dispersive Fraction, DF). It seems likely that it is these hydraulic dead zones that could act as refugia for living organisms, since they would be 'stored' in the reach along with the water and non-living particles. Lancaster & Hildrew (1993) used solute transport experiments to examine transport processes in nine streams in the UK and successfully quantified the proportion of water in transient storage, i.e. in hydraulic "Dead Zones".

An alternative, though related, approach to the physical assessment of instream refugia is to measure the forces of flow at separate points on the bed. Points that retain low shear stress even at high flows would be candidate refugia (and could act as the Dead Zones measured by the transient storage models). It is further possible to characterise flow conditions by measuring shear stress in individual patches using FST hemispheres (Statzner & Müller, 1989). The frequency distributions of those measurements over a stream reach can then be examined. Although this type of

measurement does not reflect the shear stress applied to individual invertebrates or particles, it does describe the habitat at a coarser scale and is useful in this respect.

Although these methods had successfully shown that there were differences in the hydraulics between streams, and that the proportion of non-flowing water could be calculated (as the DF), it was still unclear whether such dead zones were important to invertebrates. Winterbottom *et al* (1997a) recently used an experimental approach to address this question. They introduced two different types of cages with substratum into each of two streams with differing hydraulic characteristics. One type of cage had a wide mesh which did not alter the flow inside the cage, and the other had a much finer mesh which reduced the flow inside while still allowing free access to invertebrates. Thus, one cage was an artificial flow refugium, the other a control. Winterbottom *et al*'s (1997a) week-long colonisation trials were carried out in two streams, one with a low Dispersive Fraction (few dead zones) and one with a high Dispersive Fraction. In the latter, animals accumulated in the refugium cages in much greater numbers than in the controls when a spate occurred during the 7 day exposure period. At low flows there was no difference in colonisation. In the stream with few natural refugia there was no difference in colonisation of the two types of cage. While by no means conclusive, these experiments suggest that in-stream flow refugia can be used by invertebrates and that traits favouring refugium use may be favoured in habitats where flow refugia are available.

Another important aspect of the impact of disturbance by spates is the distance organisms travel once entrained in the drift. The overall retention of organisms in stream channels is determined both by the likelihood of initial entrainment and also by the distance travelled per drift event. In field experiments Lancaster *et al* (1996, see Appendix 1) disturbed the benthos in streams with differing hydraulic transport properties, at a range of discharges. Drifting invertebrates were captured at different distances downstream from the disturbance, and an instantaneous return rate was calculated. Return rates were found to be greater in streams with a higher DF (i.e. animals were not transported so far), although there was some variability among

streams with lower DFs. This encourages the view that downstream losses of individuals due to spates could be modified by the hydraulic environment in natural channels.

A closer inspection of the Lancaster *et al* (1996) data also revealed that transport patterns differed among taxa. The return rates of leuctrid and nemourid stoneflies were compared in two streams with differing DFs. Invertebrate assemblages were very similar between the streams, reflecting their close geographic proximity and similar chemical character. Drift distances for leuctrids were closely related to the DF, indicating passive use of refugia, whereas the drift of nemourids was not correlated to the DF, indicating actively determined drift (see Lancaster *et al*, 1996 in Appendix 1 for more detailed explanation). Winterbottom *et al* (1997b) and Lancaster *et al* (1990) found a similar species-specific pattern. Thus, the biological importance of refugia may be determined in part by the species composition of individual streams.

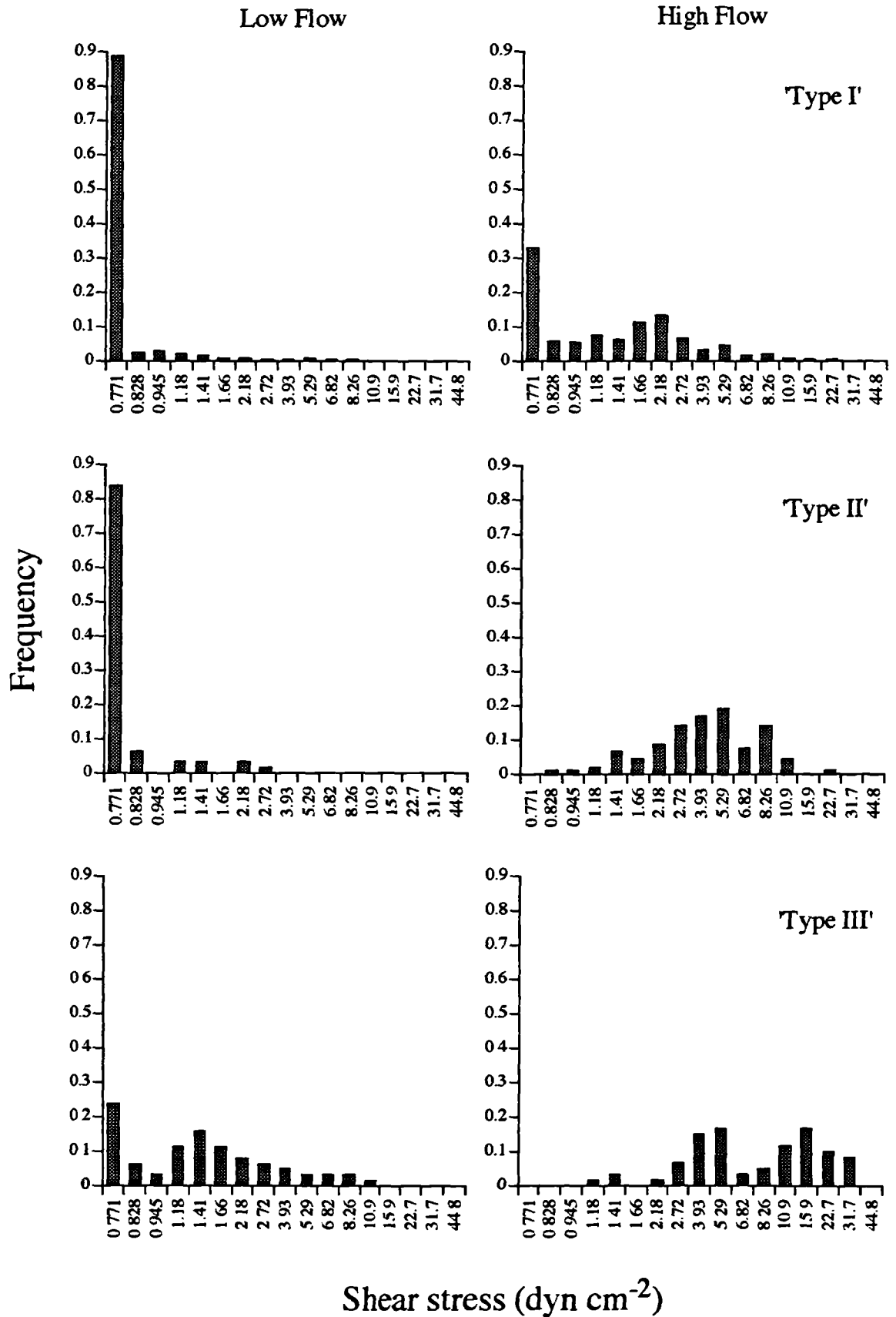
4.1.i Stream "Types"

From the nine streams they studied, Lancaster & Hildrew (1993) identified three stream "Types" that were distinguished by the frequency distribution of shear stress (measured with FST hemispheres) at different flows (Fig 4.1). Type I streams have a high proportion of low shear stress spots at low flow, and a large proportion of these are retained even at high discharge. These are the areas invertebrates may use as flow refugia. Type III streams have very few low shear stress spots even at low discharge, and a relatively high proportion of high shear stress spots. At high discharge the low shear stress spots disappear completely. Type II streams are an intermediate between the other types; at low discharge there is a relatively high proportion of low shear stress spots, at high discharge some of these are retained, but there are a much higher proportion of high shear stress spots. Type II streams can be said to resemble Type I streams at low discharge, and Type III streams at high discharge.

Figure 4.1. Shear stress distribution examples for Type I, II and III streams.

* Broadstone Stream (Type I) (low flow: 29-8-91, $Q = 0.0026 \text{ m}^3/\text{s}$; high flow: 30-3-91, $Q = 0.051 \text{ m}^3/\text{s}$),
 own data { Weirwood Road (Type II) (low flow: 9-9-94, $Q = 0.0039 \text{ m}^3/\text{s}$; high flow: 14-2-95, $Q = 0.134 \text{ m}^3/\text{s}$) and
 Withyham Green (Type III) (low flow: 6-9-94, $Q = 0.081 \text{ m}^3/\text{s}$; high flow: 10-2-95, $Q = 1.147 \text{ m}^3/\text{s}$).

* Data from Lancaster & Hildrew, 1993.



From a biological aspect, Type I streams have the highest proportion of potential flow refugia that may be used by the invertebrates during high flow events. Type III streams at high flow offer few flow refugia to invertebrates, at least at the spatial scale assessed.

4.1.ii Refugium availability as a continuous variable

Lancaster & Hildrew (1993) acknowledged at the outset that with a larger sample the pattern of shear stress among streams, that they placed into the three categories, would probably prove to be continuous. Since low shear stress (or hydraulically undisturbed) spots at high discharges may act as refugia, it is possible to use the proportion of such low shear stress spots at high discharge as a measure of refugium availability. Such a measure would place streams along a continuum of refugium availability rather than in one of the three categories.

The question then arises as to at which 'high' discharge it is appropriate to make comparisons amongst streams. The discharge chosen for comparison should, in relative terms, be equally high in all streams (i.e. at a similar fraction of peak flow). In a single local area (such as the Ashdown Forest, for instance) all the streams are likely to be at similar relative discharge on the same day. For a substantial number of sites, however, it is not possible to measure shear stress frequency distributions on the same day (each site takes about 4 hours). The hydraulic model of Lamouroux *et al* (1992), however, allows predictions of shear stress frequency distributions at any discharge, using some simple physical measurements. Thus, though estimates of shear stress distributions could not be made empirically at exactly the same relative discharge at all sites, it was possible to use the model to predict them. This approach was used in my study to place the streams along a continuum of refugia.

The availability of flow refugia may "buffer" the effects of disturbances, so a measure of refugium availability could be a useful second axis for a Habitat Templet (with the frequency of disturbance as the first). In this Chapter, therefore, I present a set of measurements used to characterise the availability of instream refugia at 20

sites in the Ashdown Forest, namely the shear stress frequency distributions at different flows.

4.2 Methods

4.2.i Stream "Types"

Shear stress distributions were obtained empirically using FST hemispheres (Statzner & Müller, 1989). These hemispheres are all the same size and shape, but they vary in density so that a different force is required to move each one. They have been calibrated in a flume, so the critical shear stress is known for each hemisphere (Statzner *et al*, 1991). Hemisphere number 1 is the lightest, number 24 the heaviest.

In the stream, a lead plate was placed on the substratum horizontally. There are two small spirit levels on the plate to make this easier. Hemispheres were then placed on the plate in turn, and the heaviest hemisphere to move was recorded.

Three or five measurements were made on transects across the stream channel depending on channel width. One hundred measurements were taken in all, with a spacing between the transect of approximately 1.5 channel widths. If a spot could not be measured because it was either too deep (above the shoulder) or too shallow (not covering the hemisphere completely), the spot was recorded as blank, but included in the 100 total. Thus it is possible to finish with a total of less than 100 'real' measurements. If hemisphere number 1 did not move, the spot was recorded as 0. Most streams were measured twice, at 'high' and 'low' flow. Streams were then attributed to one of the three 'Types' by the shape of the shear stress frequency distributions at low and high flow (see Fig. 4.1). Discharge was measured at each stream on each sampling occasion. The methods for measuring discharge are described in detail in Chapter 3.

4.2.ii Refugium availability as a continuous variable

The model of Lamouroux *et al* (1992) calculates the frequency distribution of shear stress (hemisphere numbers) in a stream segment. One of the parameters used in

the model is highly correlated with the mean Froude number, which is estimated by the discharge, water depth and surface width measurements of the stream segment. To ensure that the model fitted well to the data, a comparison was made between measured and predicted hemisphere distributions. To achieve this the discharge on days when I made my own hemisphere measurements was used to model shear stress distribution in the same channel. The model fitted well at high discharges at most sites but rather poorly at lower discharges, consistently underestimating the proportion of low shear stress spots (Fig. 4.2). Since it is the proportion of low shear stress spots at high discharges that are of interest, however, the model provided reliable predictions.

As explained in the Introduction to this Chapter (see 4.1.ii) to obtain a continuous measure of refugium availability using Lamouroux *et al's* (1992) model, we need to choose a common relative high discharge. Eighty percent bankful discharge was chosen as an arbitrary measure. This discharge was reached between 1 and 12 times a year in most streams.

4.3 Results

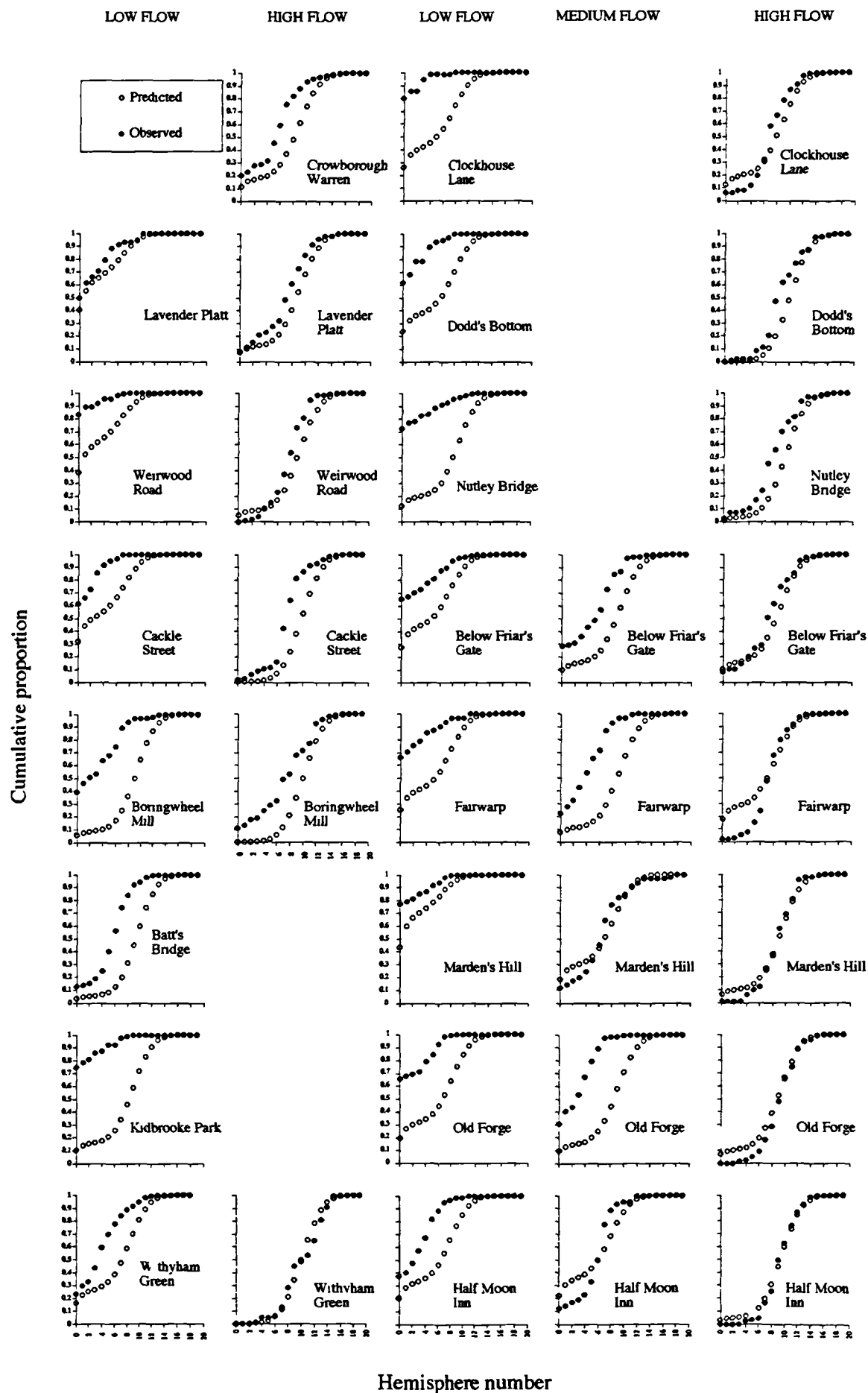
4.3.i Stream "Types"

Results of the shear stress distribution analyses can be seen in Figs 4.3-4.7, and are summarised in Table 4.1. The three streams in Fig 4.3 all resemble the Type I streams of Lancaster and Hildrew (1993). Figs 4.4-4.6 all resemble Type II streams, and Fig 4.7 Type III streams. Frequency distributions of shear stress at Old Lodge (I), Broadstone Stream (I), Maresfield (II), Lone Oak (II) and Marsh Green (III) were all measured by Lancaster & Hildrew (1993), so these streams were not remeasured.

Some of the streams could not be classified to type from data from two days only, so a third measurement (at a lower discharge) was required (Figs 4.6 and 4.7). Only one measurement was made for Kidbrooke Park, Crowborough Warren (Fig. 4.3) and Batt's Bridge (Fig. 4.7). These were Type I and III streams, and could be classified from only a single measurement (Fig. 4.1). Thus, Kidbrooke Park had a

The sites measured by Lancaster and Hildrew (1993) are not shown (Broadstone Stream, Lone Oak, Old Lodge, Maresfield, Marsh Green). Hence, only data for 16 sites are presented here.

Fig. 4.2. The relationship between the observed shear stress distributions and those predicted using the model of Lamouroux *et al* (1992) for 16 sites in the Ashdown Forest survey.



derived from hemispheres

Figure 4.3. Shear stress distributions for a) Kidbrooke Park, b) Broadstone Stream, c) Crowborough Warren.

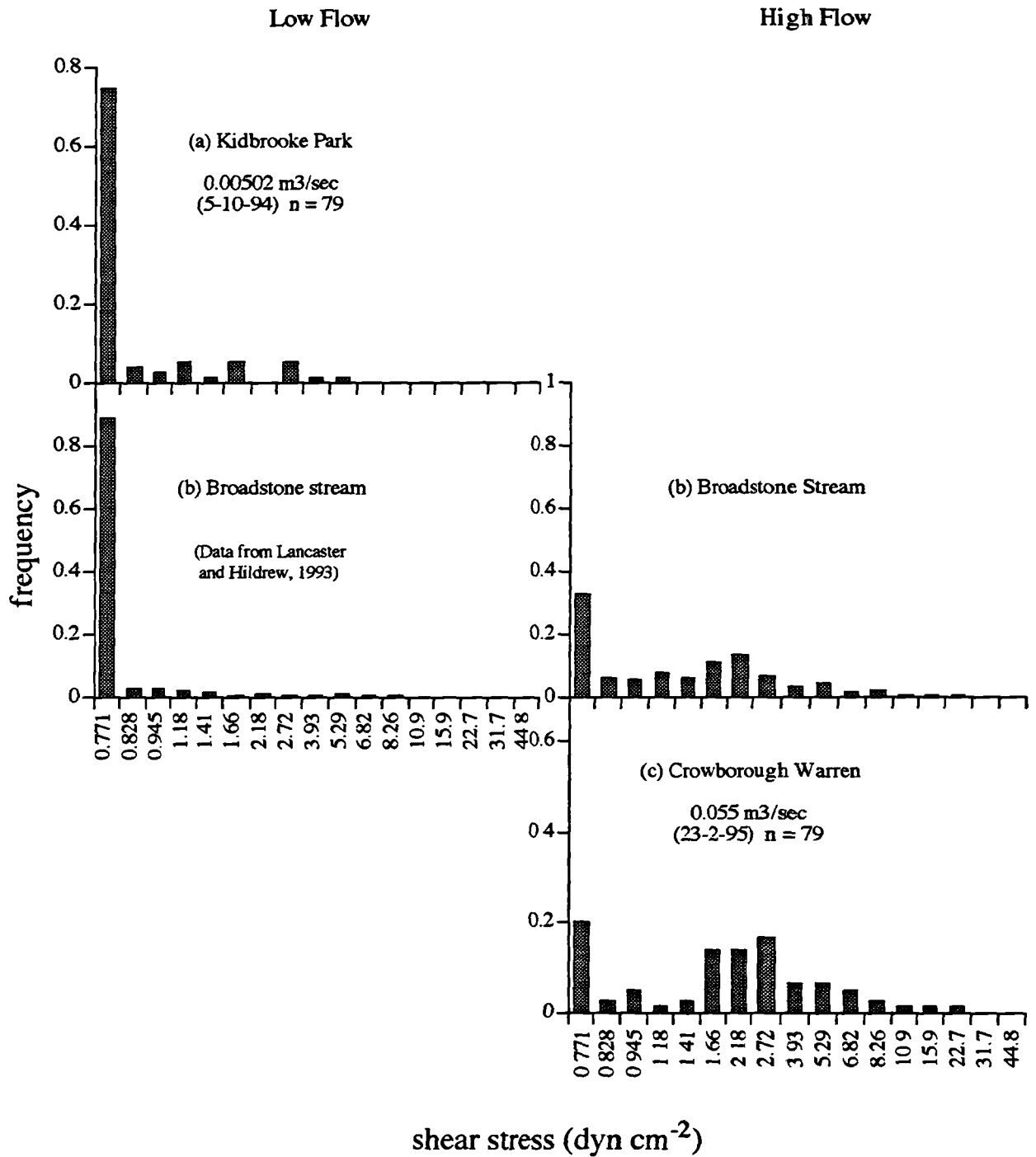


Figure 4.4. Shear stress distributions for a) Boringwheel Mill, b) Clockhouse Lane, c) Lavender Platt

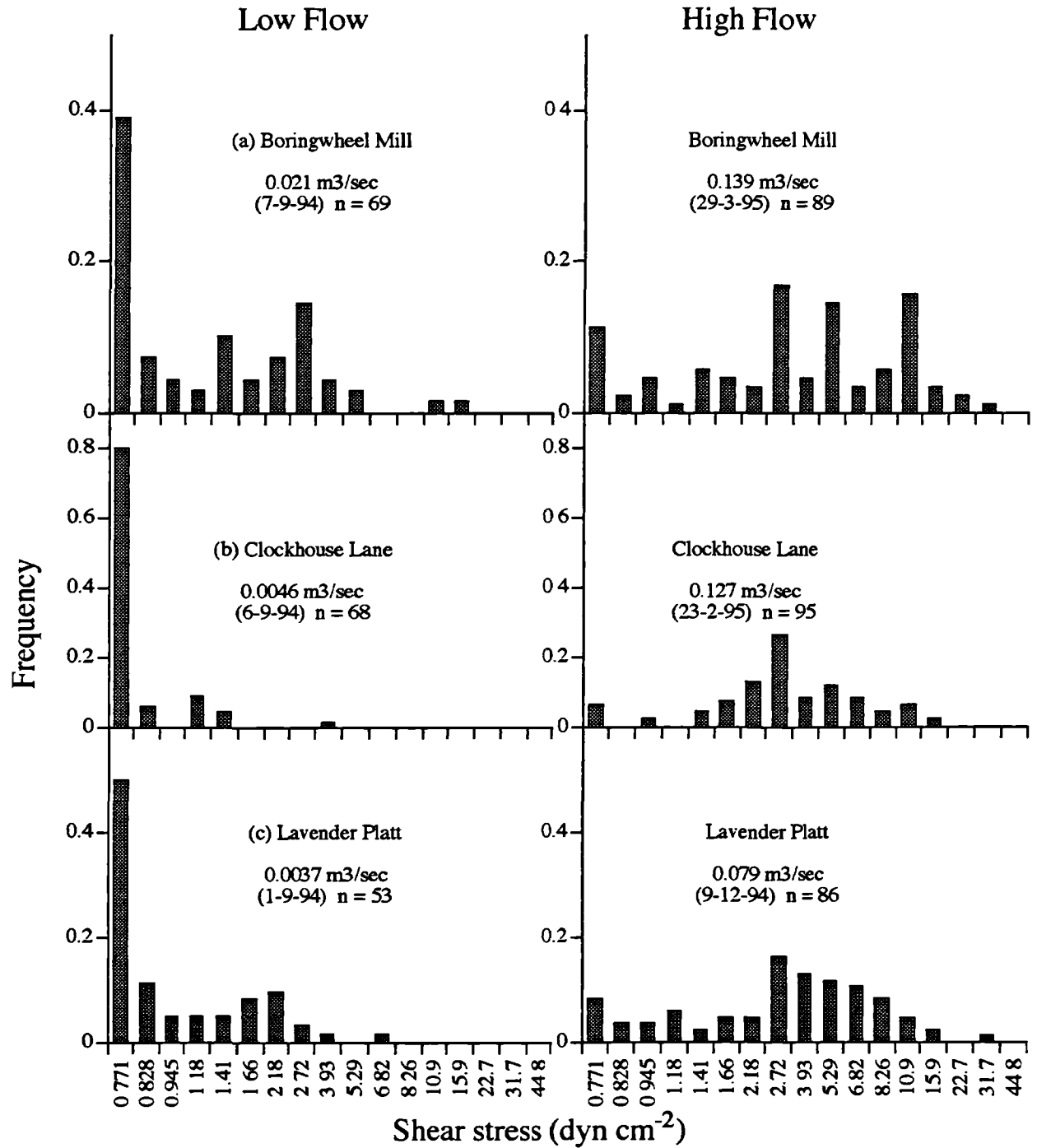


Figure 4.5. Shear stress distributions for a) Dodd's Bottom, b) Weirwood Road, c) Nutley Bridge, d) Cackle Street

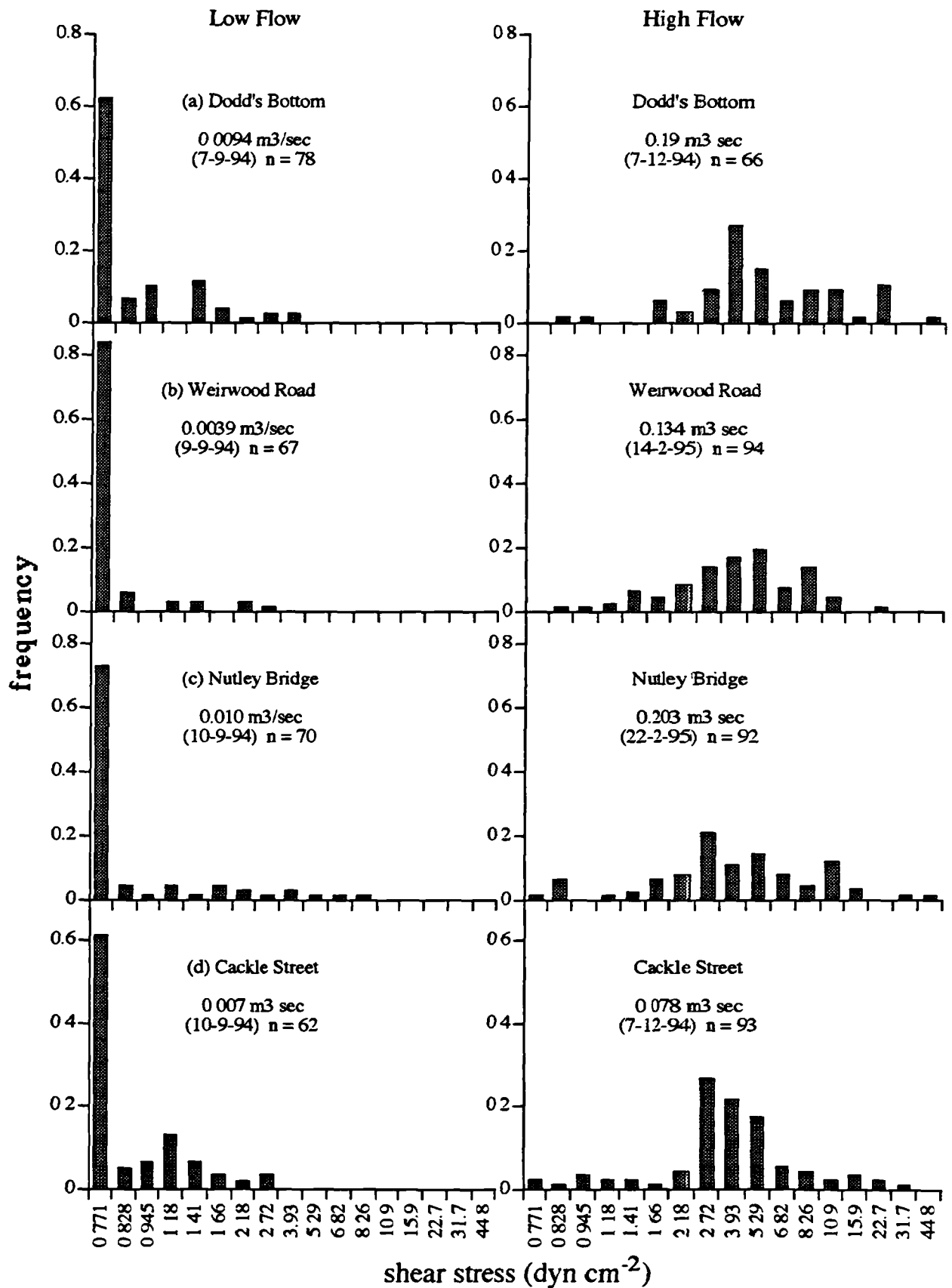


Figure 4.6. Shear stress distributions for a) Below Friar's Gate, b) Fairwarp, c), Old Forge, d) Marden's Hill

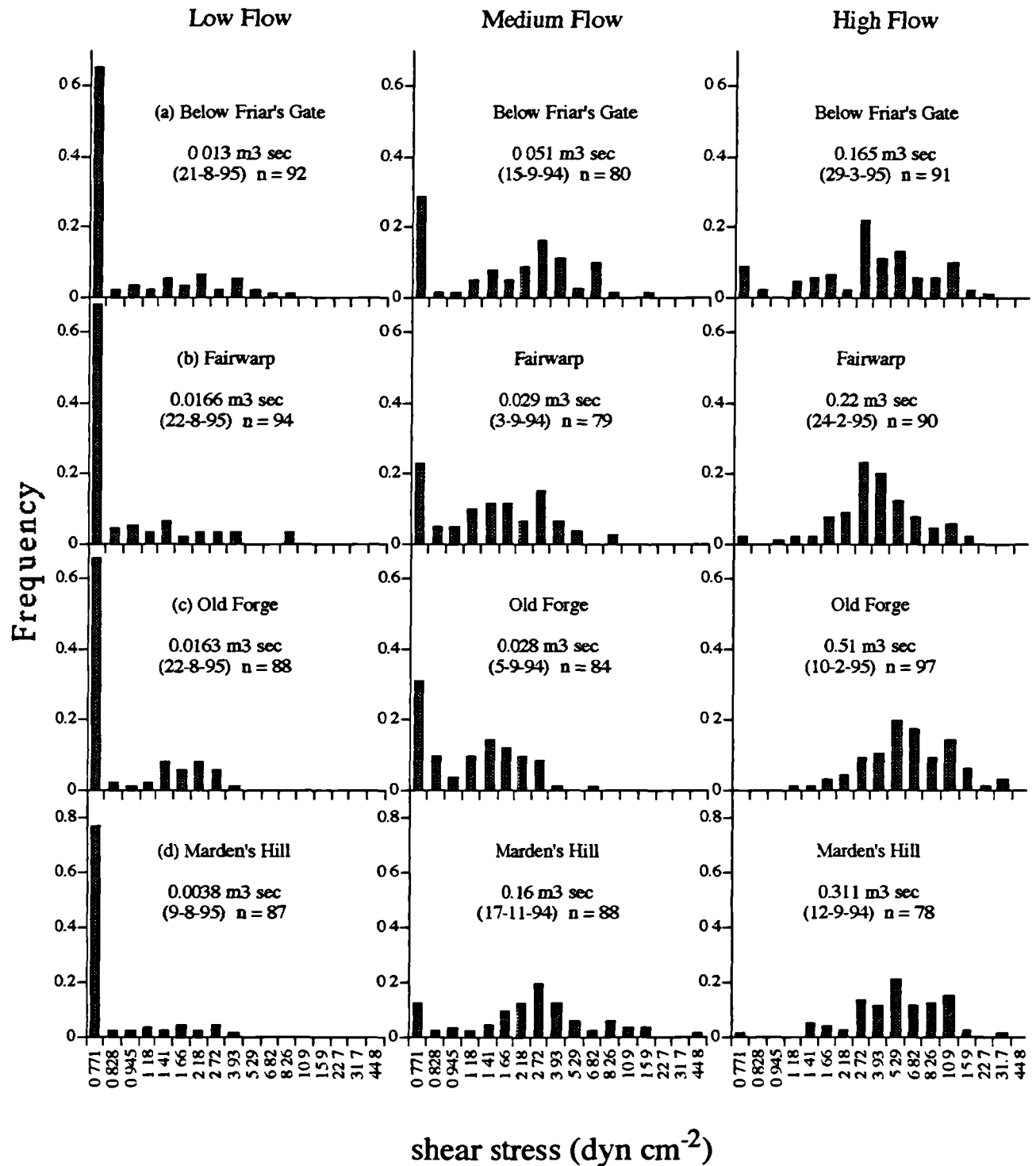
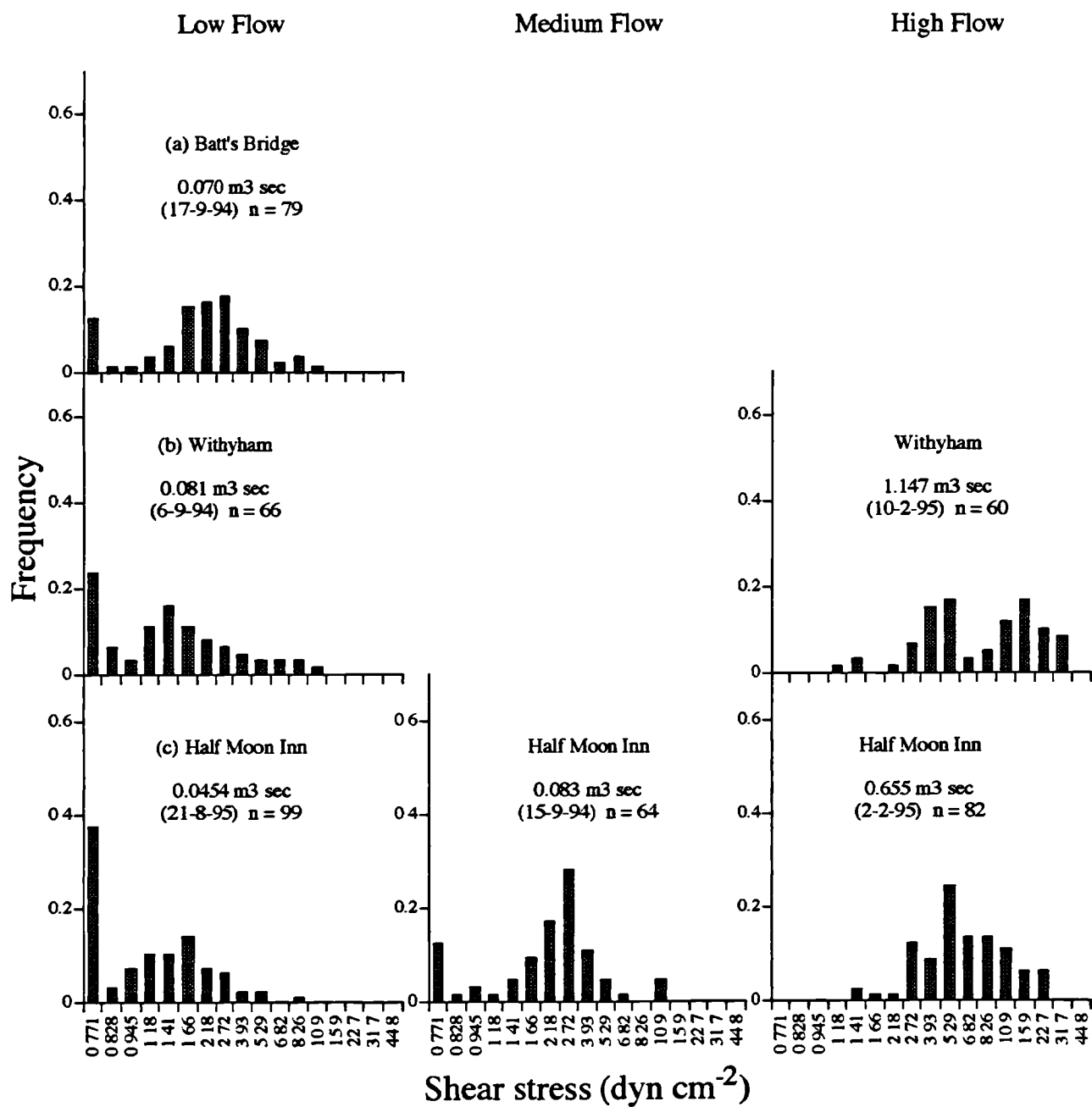


Figure 4.7. Shear stress distributions for a) Batt's Bridge, b) Withyham, c) Half Moon Inn



high a proportion of low shear stress spots at low flow (over 75%), characteristic of Type I streams especially, but occasionally also found in Type II streams. Combined with the lack of higher shear stress spots this enabled its classification as a Type I stream. Crowborough Warren had a relatively high proportion (20%) of low shear stress spots at high flow. This is characteristic only of Type I streams (Fig. 4.1). Batt's Bridge had a very low proportion of low shear stress spots at low discharge, a feature only found in Type III streams.

4.3.ii Refugium availability as a continuous variable

Stream width and depth data at 80%^{bankfull} discharge, which were needed for the model, were obtained from a logarithmic regression of my own width and depth measurements against measured discharge (Fig 4.8)*. The model of Lamouroux *et al* (1992) predicts shear stress frequency distributions for a stream segment at a given discharge. It was thus possible to predict the proportion of low shear stress spots at a given (high) discharge. The proportion of low shear stress spots arbitrarily chosen as an indication of refugium availability was hemisphere 2 or under. Thus, Batt's Bridge for example, has a high predicted proportion of low shear stress spots (Table 4.1) at 80% bankfull discharge, indicating a high refugium availability.

The model predictions do vary somewhat from the results obtained using the FST hemispheres. The discrepancy lies especially with the Type I sites, which the model does not seem to detect. However, the sites found to have the lowest proportion of low shear stress spots do generally correspond to those classified as Type III streams, with the obvious exception of Batt's Bridge (discussed below).

* Corrected regressions of the linear relationship between depth, width and discharge are shown on the pages opposite pages 75-77. The pre-correction graphs have not been removed because these show the equations used in the model, and the modelled values have not been recalculated. Modelled values using the recalculated regression equations will be used in future publications.

Fig. 4.8.i. Regression of width and depth against discharge for 21 streams, for use in shear stress model (Lamouroux *et al*, 1992). Plots are of \log_{10} values on both axes.

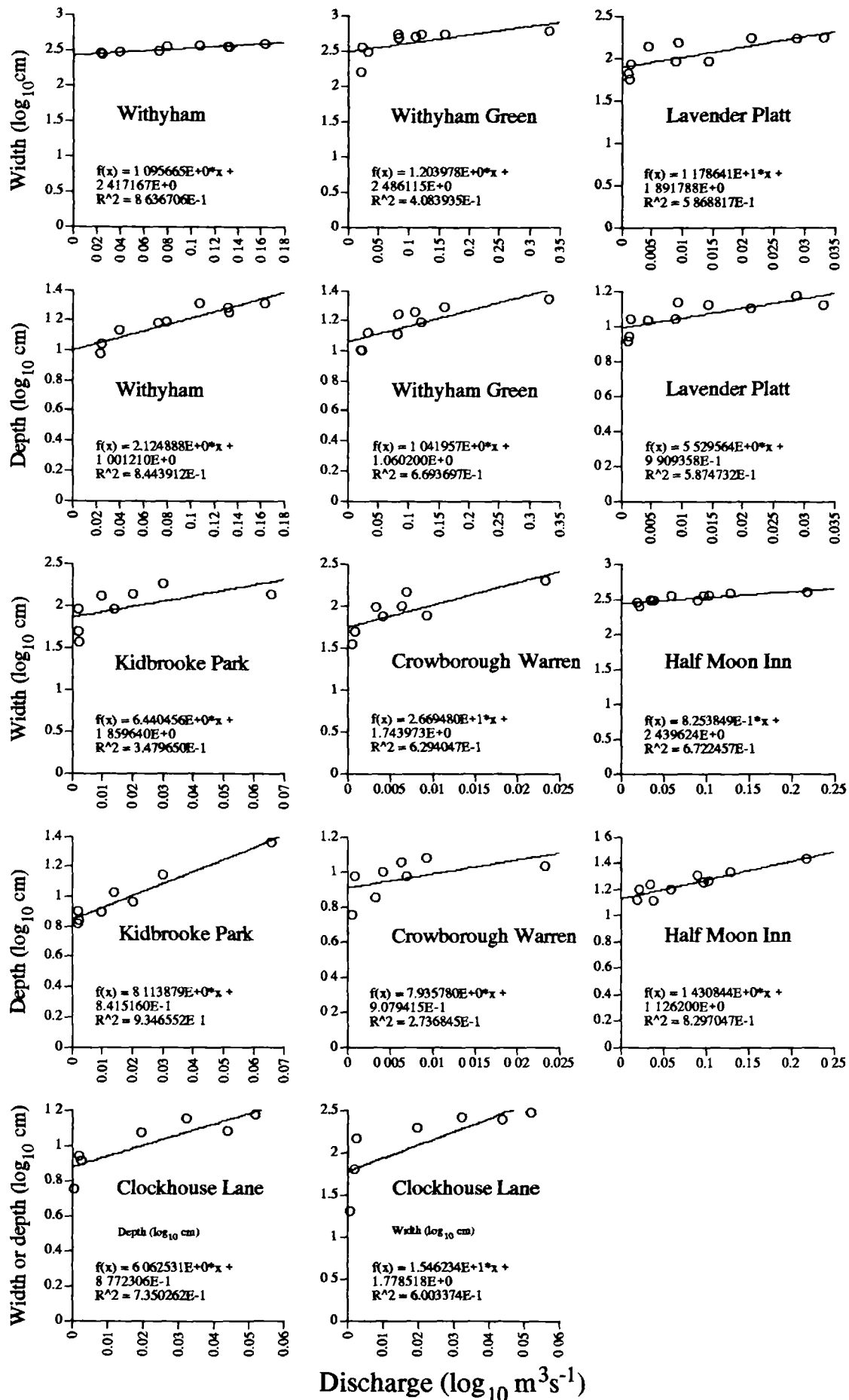


Fig. 4.8.i. Regression of discharge against width and depth for all streams, for use in shear stress model (Lamouroux *et al*, 1992). Plots are of \log_{10} values on both axes.

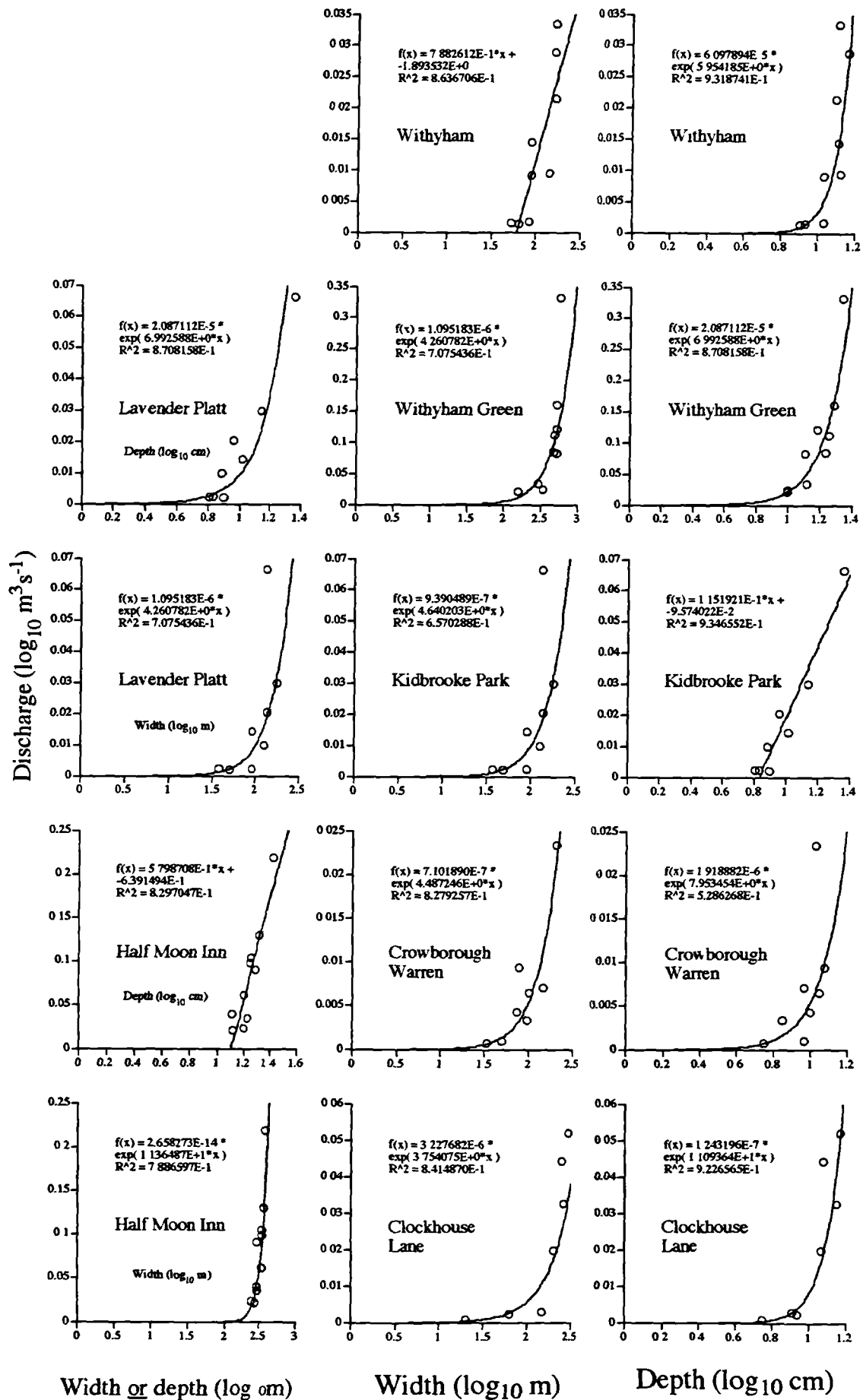


Fig. 4.8.ii. Regression of width and depth against discharge for 21 streams, for use in shear stress model (Lamouroux *et al*, 1992). Plots are of \log_{10} values on both axes.

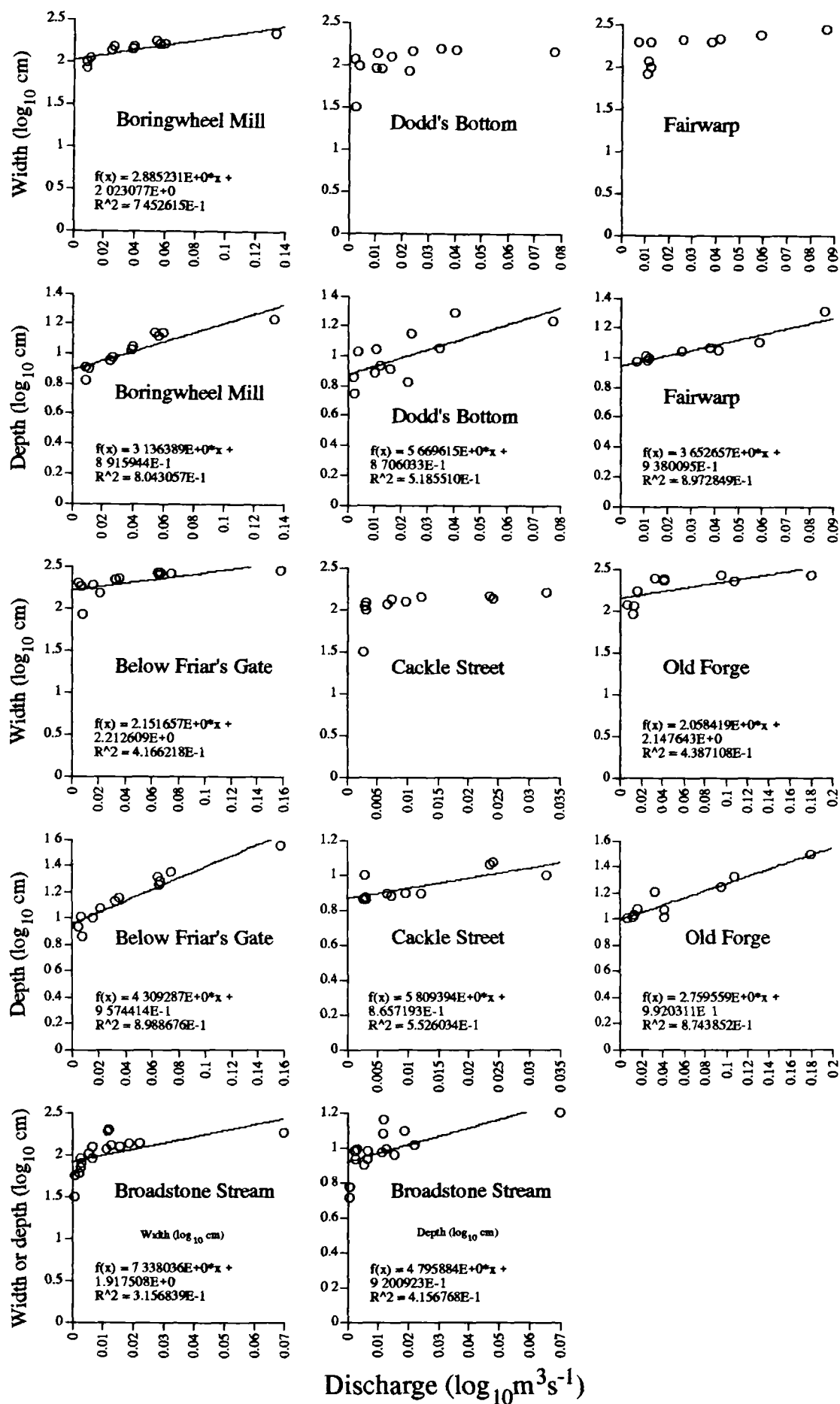


Fig. 4.8.ii. Regression of discharge against width and depth for all streams, for use in shear stress model (Lamoureux *et al*, 1992). Plots are of \log_{10} values on both axes.

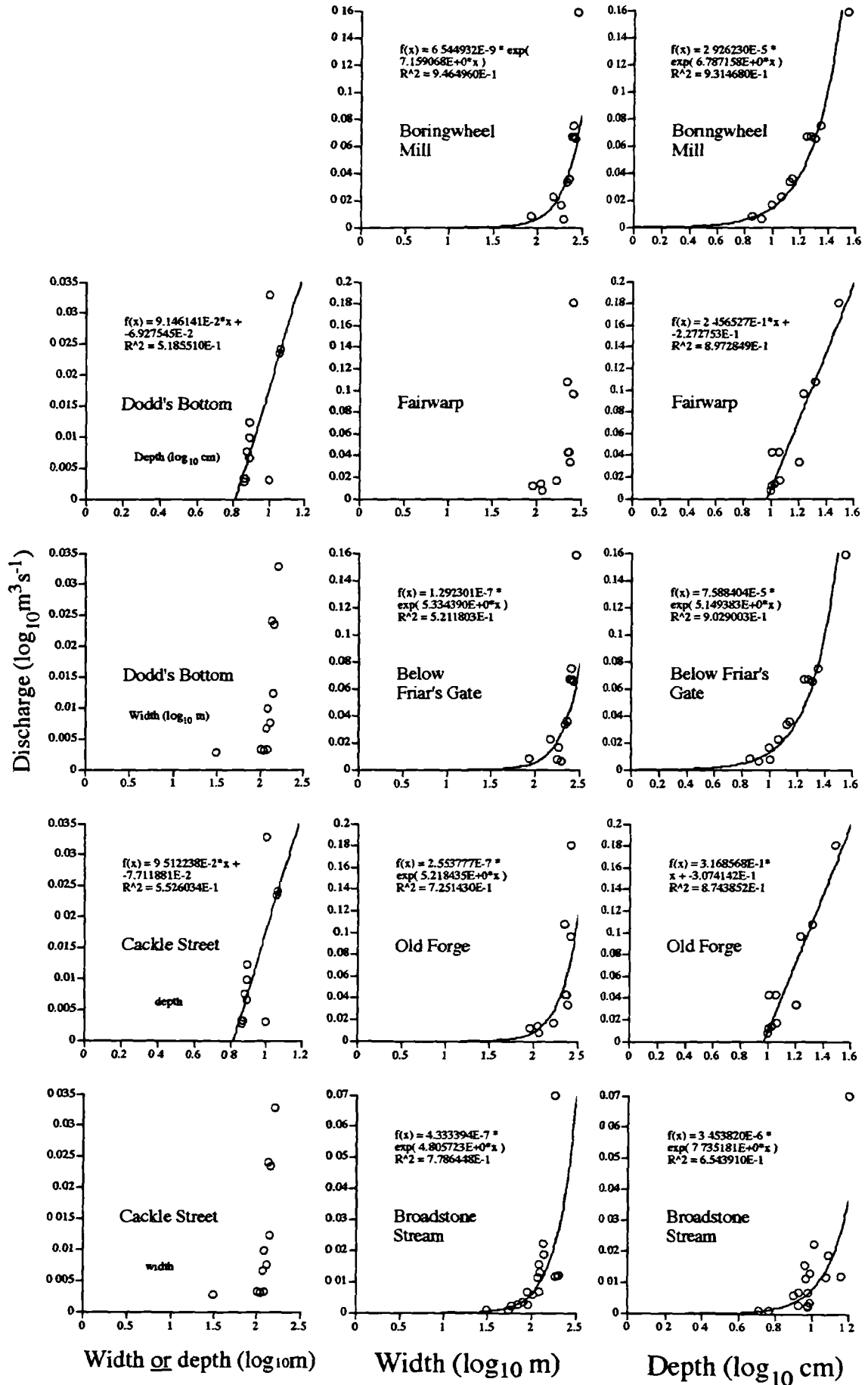


Fig. 4.8.iii. Regression of width and depth against discharge for 21 streams, for use in shear stress model (Lamoureux *et al*, 1992). Plots are of \log_{10} values on both axes.

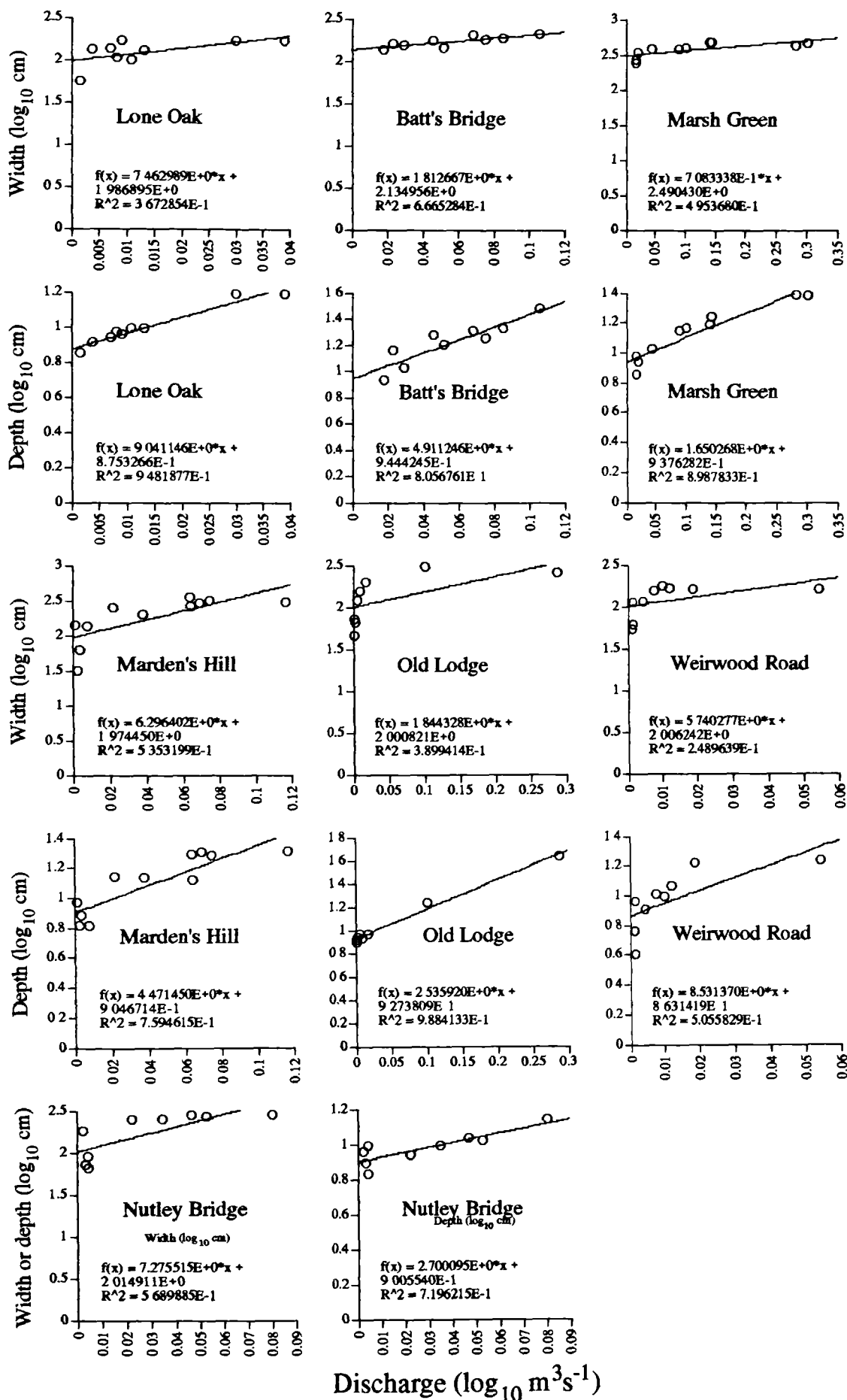


Fig. 4.8.iii. Regression of discharge against width and depth for all streams, for use in shear stress model (Lamoureux *et al.*, 1992). Plots are of \log_{10} values on both axes.

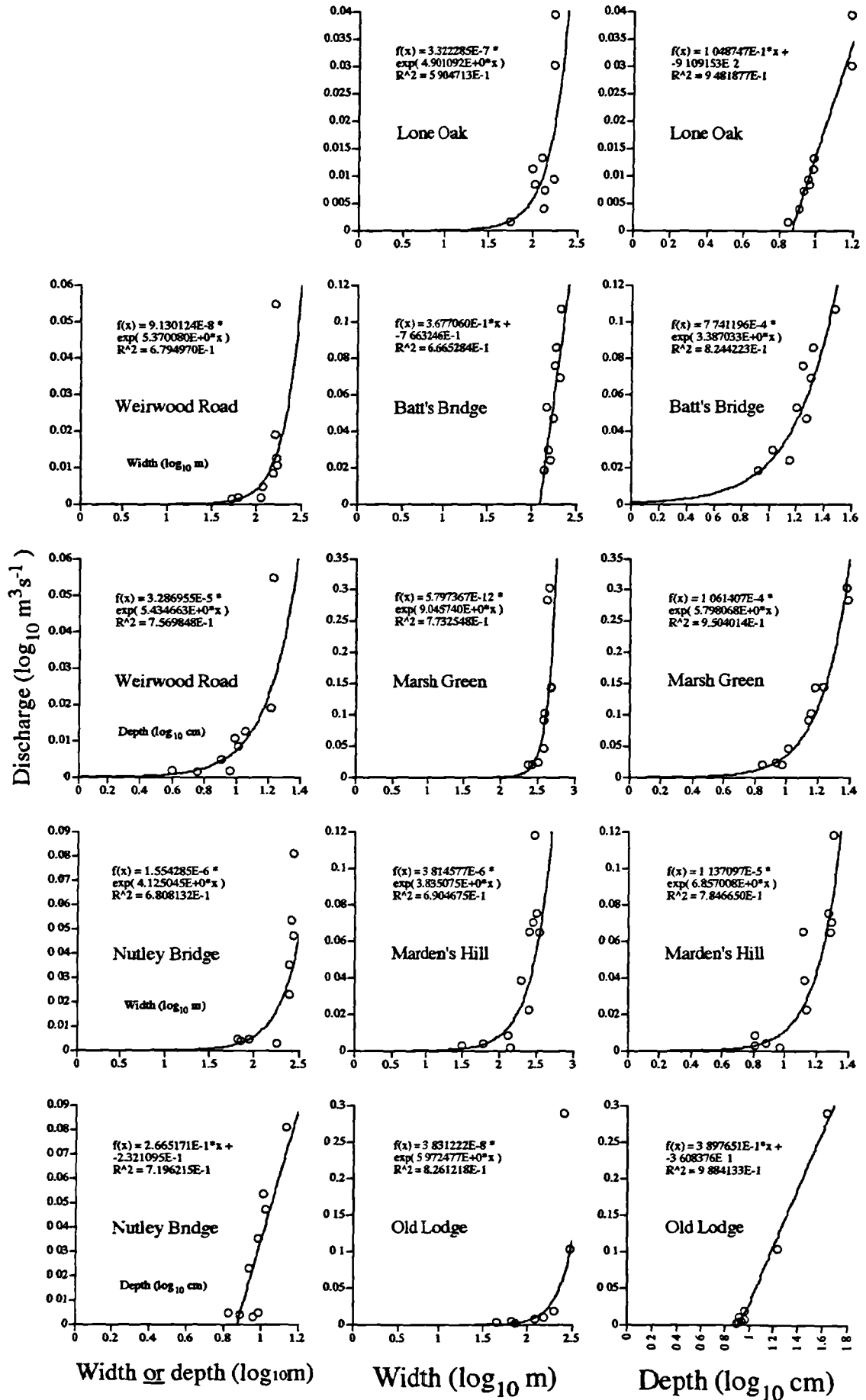


Table 4.1. Summary of refugium availability for all streams. Sites are ordered according to decreasing refugium availability as calculated by the Lamouroux *et al* (1992) model. Refugium availability is expressed as proportions of low shear stress spots: the higher the proportion, the greater the refugium availability.

Site	Modelled Refugium availability	Measured Stream "Types"
Batt's Bridge	0.4500	III
Old Forge	0.4061	II
Kidbrooke Park	0.3878	I
Nutley Bridge	0.3641	II
Dodd's Bottom	0.3608	II
Weirwood Road	0.3603	II
Fairwarp	0.3562	II
Crowborough Warren	0.3252	I
Lone Oak	0.2917	II ✓
Half Moon Inn	0.2636	III
Broadstone Stream	0.2505	I ✓
Marden's Hill	0.2472	II
Clockhouse Lane	0.2468	II
Below Friars Gate	0.2448	II
Lavender Platt	0.2312	II
Cackle Street	0.2155	II
Old Lodge	0.1188	I ✓
Withyham	0.1060	III
Withyham Green	0.0913	III
Marsh Green	0.0055	III ✓
Boringwheel Mill	0.0003	II

(✓ signifies streams classified by Lancaster & Hildrew (1993))

4.4 Discussion

A discrepancy was found between the results of the two methods at Batt's Bridge and for the Type I streams. Batt's Bridge has a small, uniform substratum with few particles protruding above the laminar layer, and very little woody debris. The hemispheres, however, do protrude above the laminar layer and create turbulence, so the shear stress measured by them may be higher than that actually working on the substratum. The proportion of low shear stress spots may also be slightly overestimated by the model for this site; Lamouroux *et al*'s model was created from data gathered in mountain streams and it may not be applicable in fine-sediment streams such as Batt's Bridge. The very homogenous structure of the substratum probably offers less refugia than predicted by the model. As substratum particle size in part is a product of the shear stress working on the bed, the modelled predictions may be more accurate than those actually measured with the FST hemispheres.

The model does not distinguish the Type I streams from the others. It is possible that this is a reflection of the poor fit of the shear stress predicted by the model at low flow compared to that measured by the hemispheres. It could also be an artefact of trying to determine stream reach characteristics from localised measurements. The Type I streams investigated in this study generally have a very heterogenous substratum, have a high proportion of woody debris and tree roots in the channel, and are not always predictably sluggish (Old Lodge). When width, depth and velocity measurements are taken to calculate discharge, a section is usually chosen that is as uniform as possible to calculate the most accurate discharge. Especially in streams such as Old Lodge, this one set of measurements might give the impression that the stream has uniformly high average shear stress, so basing the model on these data most likely underestimates the hydraulic heterogeneity. It seems likely that because of this the model does not distinguish between Type I and II streams.

The shear stress model (Lamouroux *et al*, 1992) is based on only three variables (velocity, depth and width) (see Section 4.2.ii). In other words, stream reach

characteristics are predicted from localised measurements. Although this may cause flow refugia to go undetected as explained above, it may be a powerful method to use in isolated small-scale experiments. The data used for the model in Boringwheel Mill were measured in a fast-flowing narrow section. This section was the same as was used for the tracer particle movement in Chapter 3, and the high degree of disturbance determined corresponds to the very low proportion of low shear stress spots predicted by the model.

Before choosing one of these methods for estimating refugium availability, it is important to have a definite question in mind. The modelled shear stress distributions seem most useful for small-scale experiments in coarse gravel bed streams, where only an isolated section of stream is used and considered important. As it is a very simple and quick method, it may also be useful where, for example, many streams or stream segments are to be compared. For the purpose of analyses it is often advantageous to obtain continuous measurements, rather than categorical ones, such as Type I, II and III streams. However, the model does not seem accurately to predict shear stress in complex heterogenous channels.

Hemispheres, on the other hand, because they are used over a longer stream reach and are affected by localised turbulence and wakes, are likely to reflect whole stream reach characteristics more accurately. So, if larger-scale comparisons are to be made, this method should be considered. The hemispheres highlight the hydraulic regime of the stream more accurately where as, especially at low flow (Fig. 4.2), the model underestimates the proportion of low shear stress spots. Again, hemispheres work best in coarse gravel bed streams (Dittrich & Schmedtje, 1995). It is worth noting, however, that this method is very time-consuming and should be performed by the same worker to minimise between-sample error.

For the purpose of this thesis it was decided that the inability of the ^{Lamoureux} model to detect high refugium streams* (Type I) made it unsuitable for use in a habitat templet. Thus, refugium availability described as a stream "Types" (i.e. based on the empirical

* These are the streams that retain a high proportion of low shear stress spots throughout the discharge hydrograph.

measures) will be used to generate the second axis of a habitat templet, the first being disturbance frequency.

CHAPTER 5: Community persistence and species richness in relation to disturbance frequency and refugium availability.

5.1 Introduction

5.1.i Community persistence

It has now become clear that streams vary both in their disturbance regimes and their hydraulic heterogeneity. It is also known that lotic communities persist in the face of disturbance (e.g. Scrimgeour *et al*, 1988). It is, however, uncertain whether this pattern of persistence depends on the physical habitat; it is possible, for example, that community composition in 'stressed' environments fluctuates more than in less 'stressed' environments. This is a subject that has received much attention over the years (Townsend *et al*, 1987; Weatherly & Ormerod, 1990; Giller *et al*, 1991).

In 1976 Townsend *et al* (1983) sampled 34 streams in the Ashdown Forest in an early attempt to relate community structure to environmental variables. This study was followed by further surveys in 1984 (Townsend *et al*, 1987) and 1989-90 (Edmonds-Brown, 1995) in 27 and 26 streams, respectively, of those originally studied. The 1976 survey found pH to be of overall importance in determining community structure, and that low pH sites generally had low species richness and low abundance. The 1984 and 1989 surveys supported these findings about the relationship between community structures and environmental variables but also yielded data enabling a comparison of the temporal variation in the communities; i.e. a measure of their persistence. By definition, communities are persistent when their structure changes little. Townsend *et al* (1983) found a trend towards higher persistence in cool, low pH, upstream sites.

Measuring the stability, or persistence, of communities requires monitoring on at least two occasions. The time interval between sampling occasions should be long enough to ensure at least one complete turnover of the population, to avoid re-sampling within the same generation (Connell & Sousa, 1983). Usual practices of

sampling involve either a few sites on a relative high number of occasions (Giller *et al.*, 1991; Scarsbrook & Townsend, 1993), or a high number of sites on few sampling occasions (Weatherly & Ormerod, 1990). Both sampling methods result in poor replication in either time or space.

The presence of the early data in the Ashdown Forest, combined with further sampling in 1994, provided a unique opportunity to study community patterns among a reasonable sample of streams (26) over a long period of time (18 years), to relate them to various environmental variables and, especially, to the two axes of the Habitat Templet (disturbance frequency and refugium availability).

There are at least four possible patterns that might be found when comparing community persistence among streams (Table 5.1); the streams may or may not have significantly different community compositions, and they may or may not be equally persistent.

If community composition does not vary among streams, then differences in the physical variables measured cannot be of overall importance in structuring communities. If persistence is not related to the environmental variables measured (See Table 5.1a), then populations are not affected by them. If there is a difference in persistence between these communities, and it is demonstrably related to the environmental variables measured (Table 5.1b), then those communities are affected by the variables, but not sufficiently severely or for long enough to be adapted.

If there is a difference in community composition, and this is strongly related to the environmental variables measured, then the variables chosen are likely to be important. If no differences in persistence is found amongst streams (Table 5.1c) then this could indicate that communities consist of species adapted to the physical habitat, such that density independent population changes driven by disturbances are reduced. If so, patterns in such species traits should be detectable. This is discussed further in Chapter 6. If community persistence does vary significantly in relation to the physical habitat (Table 5.1d), it infers that the habitat directly influences community dynamics

Table 5.1. Possible patterns in community composition and persistence.

	No differences in community composition between streams	Different community compositions between streams
No difference in persistence	a) Communities not affected by environmental variables measured	c) Environmental variables of overall importance in structuring communities. Community composition includes species with traits adapting them to key environmental variables.
Differences in persistence	b) Communities affected by environmental variables measured, but not sufficiently for species to complement change or for evolutionary adaptation to occur.	d) Communities are affected by physical disturbance and refugia but these variables do not determine the species present. The species complement is determined by other factors, such as acidity, for instance, or by biotic interactions.

in the short term, but is insufficient to change the species complement. Perhaps community composition is not simply the result of the few measured environmental variables but is more complex, involving several equally important environmental variables and/or biotic interactions.

If the environmental variables chosen causally explain the species traits represented in the community, then this would support the Habitat Templet Hypothesis. In this case the expected pattern is that represented in Table 5.1c: a difference in community composition amongst streams with differing environmental variables, but no differences in community persistence.

* The Chironomidae and other Diptera were identified to genera where possible. This level of identification was not always made in other years, and where comparisons between years consequently were not possible at genera level, or where single individuals of rare species had been reported, Chironomidae were simply divided into Chironominae, Orthocladinae and Tanypodinae.

5.1.ii Species richness

As mentioned previously, Townsend *et al* (1983) found species richness to be the lowest amongst low pH streams in the Ashdown Forest, and this pattern was confirmed by Rundle & Hildrew (1990) for the microarthropods. Some theory suggests that species richness will peak at intermediate levels of temporal and spatial variation, because competitive exclusion will reduce species richness at low levels of disturbance, and species richness will also be reduced under severe or frequent disturbances. This is the Intermediate Disturbance Hypothesis of Connell (1978; see also Hildrew & Townsend, 1987). The data gathered here can be used to provide a further test of the Intermediate Disturbance Hypothesis since I have measured both physical disturbance and species composition. Species richness will thus be determined for the 26 streams in the Ashdown Forest and compared to disturbance frequency and refugium availability.

5.2 Methods

Persistence data were available from previous work. These data consisted of five replicate Surber sample-units taken in the spring of 1976 (Townsend *et al*, 1983) and 1984 (Townsend *et al*, 1987) and in autumn 1989 and spring 1990 (Edmonds-Brown, 1995). These samples were taken from riffles in twenty-six of the thirty sites described in Chapter 2. In addition, further samples were taken in May and October 1994 using identical methods. Samples were preserved in 70% alcohol in the field, and were sorted and animals identified to species level^{*} where possible in the laboratory.

5.2.i Statistics: Indices

Pairwise comparisons were made using Jaccard's and Sorensen's Indices of Similarity and Spearman's Rank Correlation Coefficient. Jaccard's and Sorensen's Indices were calculated manually, and Spearman's Rank was calculated using the program SYSTAT (Wilkinson, 1992). Jaccard's and Sorensen's Indices both compare

the number of species in common between the two samples ^(=years) compared to the total found in each. Formulae used were:

Jaccard's Index of Similarity: $C_J = c/(a+b-c)$ (Southwood, 1978)

Sorensen's Index of Similarity: $C_S = 2c/(a+b)$ (Sorensen, 1948)

where: a = the number of taxa found in year a

b = the number of taxa found in year b, and

c = the number of taxa found in both years a and b.

Both indices take on a value between 0 and 1, where 1 indicates complete similarity and 0 no similarity.

Spearman's Rank Correlation Coefficient compares the ranking of the species with regards to abundance between the two years compared. Only species that are present in both years are used. The formula is:

Spearman's Rank: $r_s = 1 - (6 \sum d_i^2) / n(n^2 - 1)$ (Spearman, 1904)

where: d_i is the difference in the ranks. The significance of the correlation depends on n, the number of species found in common (Zar, 1984). Spearman's Rank takes on values between -1 and 1, where 1 indicates perfect positive correlation and -1 perfect negative correlation. Jaccard's and Sorensen's thus compare only presence/absences, whereas Spearman's compares relative abundances.

5.2.ii Statistics: Non-parametric and regression

Kruskal-Wallis one-way analysis of variance (Kruskal & Wallis, 1952) was used to test for differences in index values between sites for Jaccard's and Sorensen's Indices. A non-parametric test was used because index values cannot be assumed to follow a normal distribution, and Kruskal-Wallis was chosen because several

independent samples were compared at once. This test ranks the values and tests for differences in ranks instead of raw counts (ranking is performed on the pooled data of all yearly combinations for each site, and does, therefore, not test for differences between years within sites). Computations are otherwise the same as for analysis of variance.

Jaccard's and Sorensen's Indices were also plotted against stream 'Type', a continuous measure of refugium availability, disturbance frequency, pH, July temperature and distance from source, independently. This was done to test for direct linear relationships between community persistence and each independent environmental variable.

5.2.iii Statistics: Multivariate

To test for non-linear relationships the raw data were analysed using the program CANOCO, CANONical Community Ordination by [partial] [detrended] [canonical] correspondence analysis (ter Braak, 1988), which is an extension of the widely-used program DECORANA (Hill, 1979). Regression is used to display a linear relationship between an abundance value of a species and an environmental value. Often the relationship is not linear, but may be unimodal; a Gaussian relationship is shown. Ordination is very much like regression analysis, the major difference being that many variables are considered simultaneously.

Indirect gradient analysis was used on the raw data. It attempts to uncover the underlying structure of the data, and assumes it is determined by a few unknown environmental variables; the 'latent' variables. The ordination is constructed to 'best' explain the species data. There are, of course, many variables that affect species data; ordination tries to find a few that are the most important and positions the species data in relation to them. Ordinations are most easily understood in biplots. The biplots in this thesis were created using CALIBRATE (Juggins & ter Braak, 1997). Axis 1 is the most important latent variable and it creates maximum dispersion of the species data along this axis. Axis 2 is second most important and separates the

species along the y-axis. The Eigenvalues indicate how good a fit the latent variables are to the data. Eigenvalues are simply the total sum of squares of regressions of species abundances on the latent variables. They are expressed as the percent of the total variance in the species data. CANOCO calculates Eigenvalues for each axis and, often, most of the variance is explained by the first two axes.

As mentioned above, sometimes relationships are linear between species data and environmental data while in other instances there is a unimodal, or Gaussian, relationship. Before deciding on the use of an ordination technique, it must be decided whether the species data show a unimodal or linear response. The first test should be a DCA (Detrended Correspondence Analysis). This is a unimodal response model (Table 5.2) and, if the gradient length for Axis 1 is high (usually above 2 standard deviations), it indicates that the model separates the species data well along that axis

Table 5.2. Multivariate analyses in CANOCO.

	Linear response model	Unimodal response model
Indirect gradient analysis	PCA	CA / DCA
Direct gradient analysis	RDA	CCA / DCCA

and that a unimodal response model is appropriate. If the gradient length is low, however, then there is poor separation along the first axis and a linear response model should be used. For values between 1.5 and 3.0 standard deviations both are effective.

One of the advantages of CANOCO over DECORANA is that it provides an alternative method of detrending. Species data often show an 'arch' effect when the CA (Correspondence Analysis) is plotted. This is caused by a mathematical artefact; an 'edge' effect when the programme maximises the dispersion by 'weighted averaging'. This effect can be avoided by non-linear rescaling, or detrending, of the first CA axis, which is done in DCA. A rule of thumb is to perform a CA first and, if the arch effect appears in the biplot, then redo the analysis using DCA instead.

Direct gradient analysis in principle is much the same as indirect gradient analysis, but is used when environmental variables have been measured and one wishes to know how much of the variance in the species data is explained by those variables. The ordination is now constrained by environmental variables, and the species data are placed in relation to the information given. This may be a useful technique, but it is important to remember that the environmental variables chosen may not be the most important in determining overall differences in the species data. The ordination can be said to be 'artificial' as it is a forced relationship that is shown. An indirect ordination is more likely to show 'real' differences in species data.

Direct gradient analysis also allows for covariables. This is useful, for example, if one environmental variable is known to be very important (e.g. pH) in determining community composition, but one wishes to examine the effects of other environmental variables independently of pH. A straight CCA with no covariables will separate the species data out along Axis 1, which is strongly correlated to pH. Any other trend amongst species data and environmental data is less apparent. If pH is entered as a covariable, however, the CCA will consider the relationship between species and environment without the effect of pH.

Principal Components Analysis (PCA) works in the same way as CA and DCA, and RDA (Redundancy Analysis) works the same way as CCA (Canonical Correspondence Analysis) or DCCA (Detrended Canonical Correspondence Analysis). RDA is basically a constrained PCA, CCA is a constrained CA, and DCCA a constrained DCA (Table 5.2).

5.2.iv Stepwise multiple regression of species richness

Stepwise multiple regression was performed on the species richness data for all 26 streams on each sampling occasion from 1976-94 using the statistics package SYSTAT (Wilkinson, 1992). Before analysis the disturbance frequencies (proportions because measured as days per year) were Arcsine transformed using Freeman and Tukey's (1950) transformation:

$$p' = 0.5 [\arcsin \sqrt{x/(n+1)} + \arcsin \sqrt{(x+1)/(n+1)}]$$

An Arcsine transformation on its own does not work well at the extreme ranges of values. Because the actual proportions are known in this case (days/year = x/n), and some very large and small proportions are present in the data, this transformation is preferred (Zar, 1984). Stream 'Type' was entered as a dummy variable, as it is categorical.

Forwards stepwise regression begins with no variables in the equation, enters the most 'significant' predictor at the first step, and continues adding and deleting variables until none can 'significantly' improve the fit.

5.3 Results

5.3.i Jaccard's and Sorensen's Indices

Jaccard's Index, over all sites, took values ranging from 0.15 to 0.69 with a mean of 0.39 (Table 5.3). Sorensen's Index was a little higher on average (range 0.26 to 0.79, mean = 0.54: Table 5.4). The Kruskal-Wallis test showed that there was no significant difference between sites for either of the Indices (Table 5.5), i.e. sites were equally persistent.

Table 5.5. Results of Kruskal-Wallis analysis of variance for between site differences in Jaccard's and Sorensen's Indices of Similarity.

	Kruskal-Wallis test statistic	DF	p
Jaccard's Index	28.082	23	0.213
Sorensen's Index	28.082	23	0.213

Persistence values, based on Jaccard's and Sorensen's indices calculated on various pairs of samples, are shown graphically in Figs. 5.1-5.4. I also calculated overall mean values (\pm SD) for each site. The sites exhibiting slightly higher standard deviations about the mean were Lone Oak, Old Lodge (i), Kidbrooke Park (i) and

Table 5.3. Jaccard's Index of Similarity for all sites and all pairwise combinations of years.

	Autumn 1976-94	Autumn 1984-94	Autumn 1989-94	Autumn 1976-84	Autumn 1976-89	Autumn 1984-89	Spring 1990-94	Spring+Autumn 1989-90	Spring+Autumn 1994-94
Lavender Platt	0.65	0.48	0.41	0.43	0.42	0.45	0.29	0.39	0.27
Weirwood Road	0.43	0.37	0.32	0.47	0.36	0.41	0.42	0.47	0.51
Kidbrooke Park (i)	0.28	0.33	0.59		0.36		0.19	0.36	0.20
Kidbrooke Park (ii)	0.32		0.42	0.41	0.37	0.40	0.44	0.33	0.23
Nutley Bridge	0.35		0.34		0.30		0.34	0.36	0.41
Old Lodge (i)	0.38	0.25	0.26	0.48	0.45	0.50	0.30	0.32	0.24
Old Lodge (ii)	0.35	0.36	0.40	0.41	0.42	0.60	0.31	0.50	0.35
Lone Oak	0.40	0.35	0.35	0.55	0.54	0.55	0.31	0.35	0.36
Crowborough Warren	0.55	0.38	0.59	0.55	0.60	0.51	0.17	0.38	0.43
Cackle Street	0.35	0.44	0.45	0.48	0.40	0.46	0.28	0.36	0.30
Dodd's Bottom	0.38	0.35	0.36	0.46	0.44	0.34			
Fairwarp	0.29	0.21	0.31	0.40	0.40	0.41	0.43	0.42	0.44
Marden's Hill (i)	0.35	0.36	0.52	0.58	0.51	0.42	0.32	0.38	0.34
Marden's Hill (ii)	0.41	0.43	0.32	0.56	0.49	0.69	0.26	0.34	0.35
Below Friar's Gate	0.46	0.35	0.37	0.39	0.31	0.40	0.23	0.36	0.38
Old Forge	0.39	0.31	0.45	0.33	0.33	0.31	0.28	0.39	0.40
Batt's Bridge	0.41	0.45	0.41	0.42	0.42	0.48			
Maresfield	0.47	0.35	0.45	0.50	0.53	0.55			
Marsh Green	0.36	0.34	0.29	0.42	0.37	0.44	0.38	0.33	0.33
Half Moon Inn	0.35	0.28	0.39	0.48	0.43	0.50	0.39	0.48	0.33
Withyham	0.38	0.43	0.40	0.56	0.32	0.38	0.25	0.40	0.34
Withyham Green	0.41	0.43	0.51	0.47	0.40	0.43	0.29	0.44	0.35
Boringwheel Mill	0.31	0.19	0.32	0.29	0.39	0.33	0.33	0.35	0.50
Broadstone Stream		0.50	0.38			0.35	0.54	0.34	0.33

Table 5.4. Sorensen's Index of Similarity for all sites and all pairwise combinations of years.

	Autumn 1976-84	Autumn 1976-89	Autumn 1984-89	Autumn 1976-94	Autumn 1984-94	Autumn 1989-94	Spring 1990-94	Spring+Autumn 1989-90	Spring+Autumn 1994-94
Lavender Platt	0.55	0.58	0.62	0.79	0.65	0.58	0.45	0.56	0.42
Weirwood Road	0.46	0.54	0.58	0.60	0.54	0.49	0.59	0.64	0.68
Kidbrooke Park (i)		0.53		0.43	0.50	0.74	0.32	0.53	0.33
Kidbrooke Park (ii)	0.50	0.54	0.57	0.48		0.59	0.62	0.50	0.37
Nutley Bridge		0.41		0.52		0.51	0.51	0.53	0.59
Old Lodge (i)	0.55	0.63	0.67	0.29	0.40	0.41	0.47	0.48	0.39
Old Lodge (ii)	0.53	0.59	0.75	0.52	0.53	0.57	0.48	0.67	0.52
Lone Oak	0.69	0.90	0.71	0.57	0.52	0.52	0.48	0.52	0.53
Crowborough Warren	0.64	0.73	0.68	0.71	0.55	0.75	0.29	0.55	0.60
Cackle Street	0.53	0.57	0.63	0.52	0.61	0.63	0.43	0.53	0.47
Dodd's Bottom	0.61	0.61	0.51	0.55	0.52	0.53			
Fairwarp	0.60	0.59	0.58	0.45	0.35	0.47	0.60	0.59	0.61
Marden's Hill (i)	0.51	0.68	0.59	0.52	0.53	0.68	0.49	0.56	0.51
Marden's Hill (ii)	0.65	0.66	0.75	0.58	0.60	0.48	0.42	0.51	0.52
Below Friar's Gate	0.42	0.46	0.55	0.63	0.52	0.54	0.38	0.53	0.56
Old Forge	0.51	0.50	0.47	0.57	0.47	0.62	0.43	0.57	0.57
Batt's Bridge	0.58	0.59	0.65	0.58	0.62	0.58			
Maresfield	0.63	0.69	0.71	0.64	0.52	0.63			
Marsh Green	0.57	0.54	0.61	0.53	0.51	0.44	0.55	0.50	0.49
Half Moon Inn	0.63	0.60	0.66	0.52	0.44	0.56	0.56	0.64	0.50
Withyham	0.48	0.49	0.55	0.56	0.61	0.58	0.41	0.57	0.51
Withyham Green	0.60	0.57	0.60	0.58	0.60	0.68	0.45	0.61	0.52
Boringwheel Mill	0.54	0.56	0.50	0.48	0.31	0.49	0.50	0.52	0.67
Broadstone Stream			0.52		0.67	0.55	0.70	0.51	0.50

Fig. 5.1. Persistence at sites, measured by Jaccard's Index of Similarity, calculated by comparing collections at various occasions between 1976 and 1994 (see x-axis labels). An overall mean \pm SD is also shown for each site.

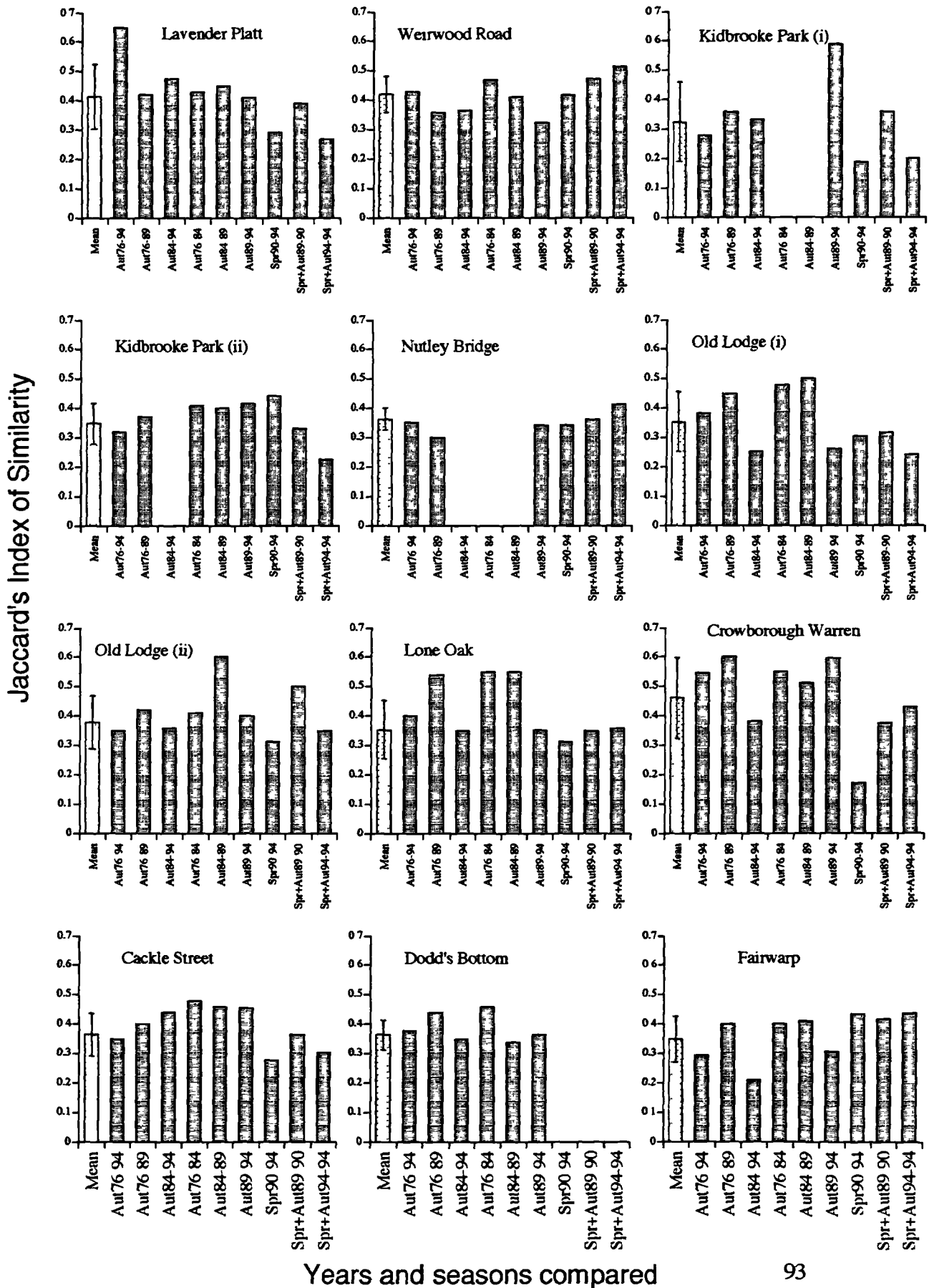


Fig. 5.2. Persistence at sites, measured by Jaccard's Index of similarity, calculated by comparing collections at various occasions between 1976 and 1994 (see x-axis labels). An overall mean \pm SD is also shown for each site.

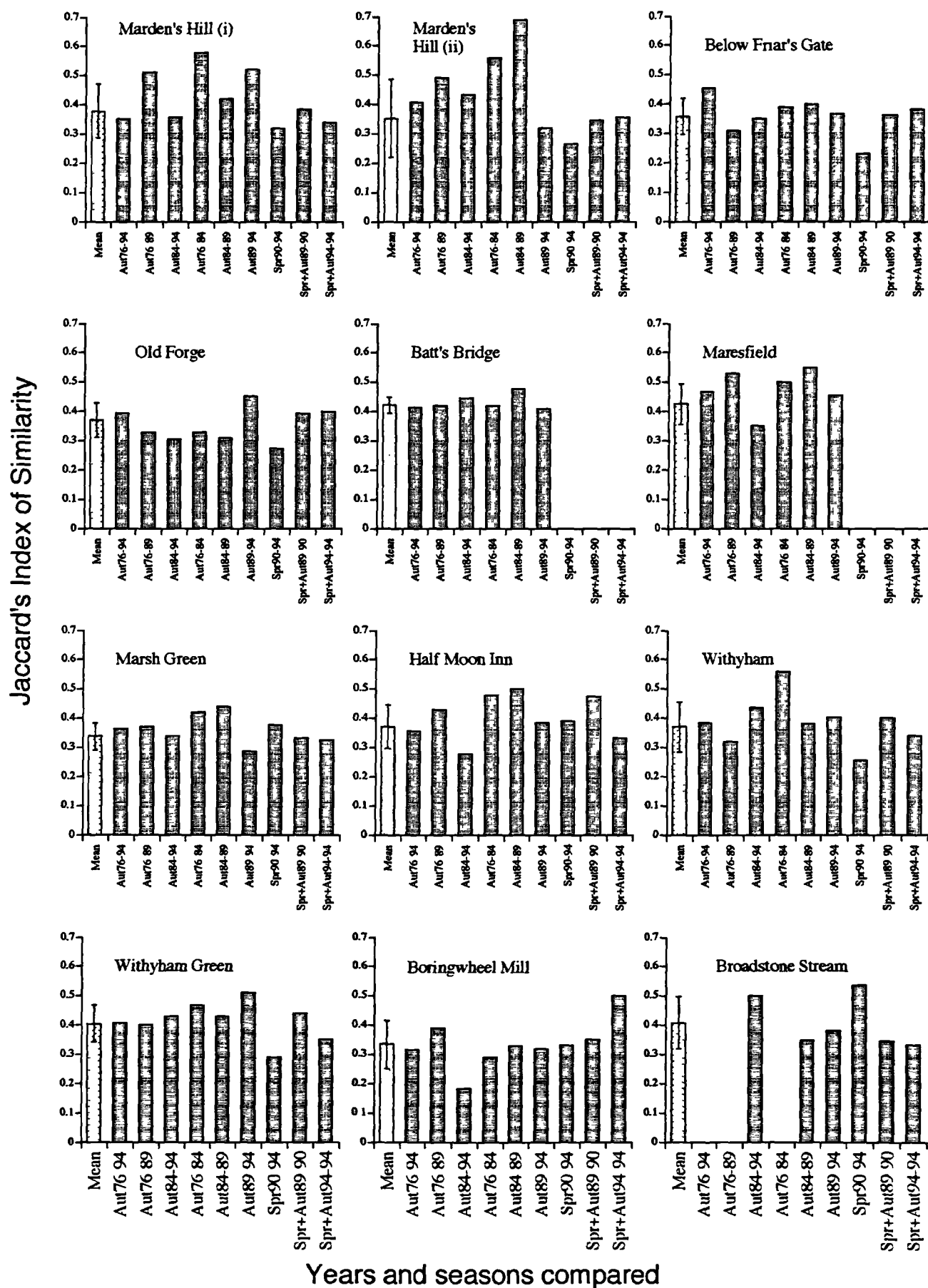


Fig. 5.3. Persistence at sites, measured by Sorensen's Index of Similarity, calculated by comparing collections at various occasions between 1976 and 1994 (see x-axis labels). An overall mean \pm SD is also shown for each site.

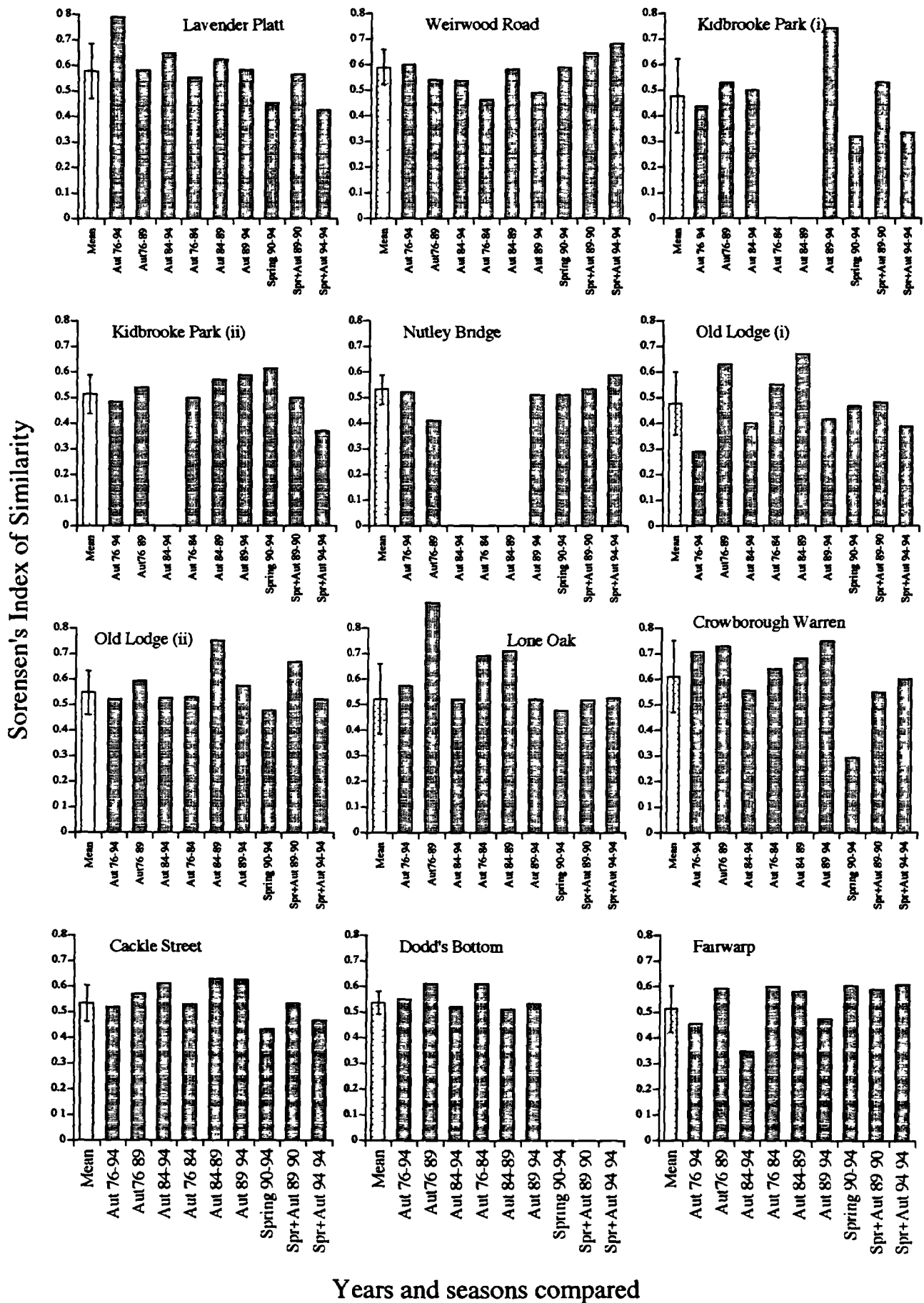


Fig. 5.4. Persistence at sites, measured by Sorensen's Index of Similarity, calculated by comparing collections at various occasions between 1976 and 1994 (see x-axis labels). An overall mean \pm SD is also shown for each site.

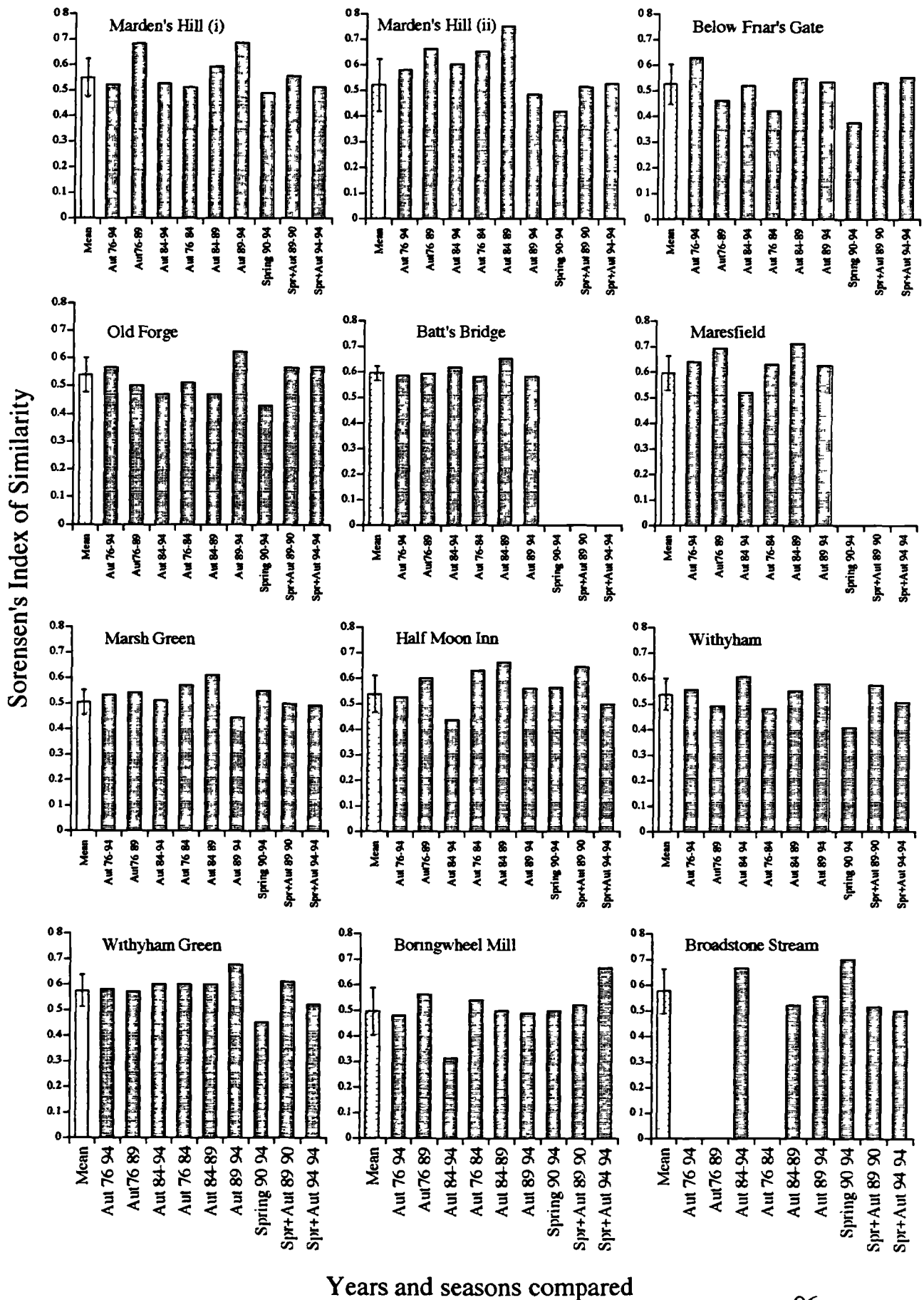


Fig. 5.5. The relationship between persistence and independent variables as measured by a) Jaccard's and b) Sorensen's Indices of Similarity. The total data set was plotted, i.e. all combinations of years and seasons at all sites. Disturbance frequency was plotted on a log scale as the value for Boringwheel Mill was two orders of magnitude higher than for most other sites.

Fig. 5.5a

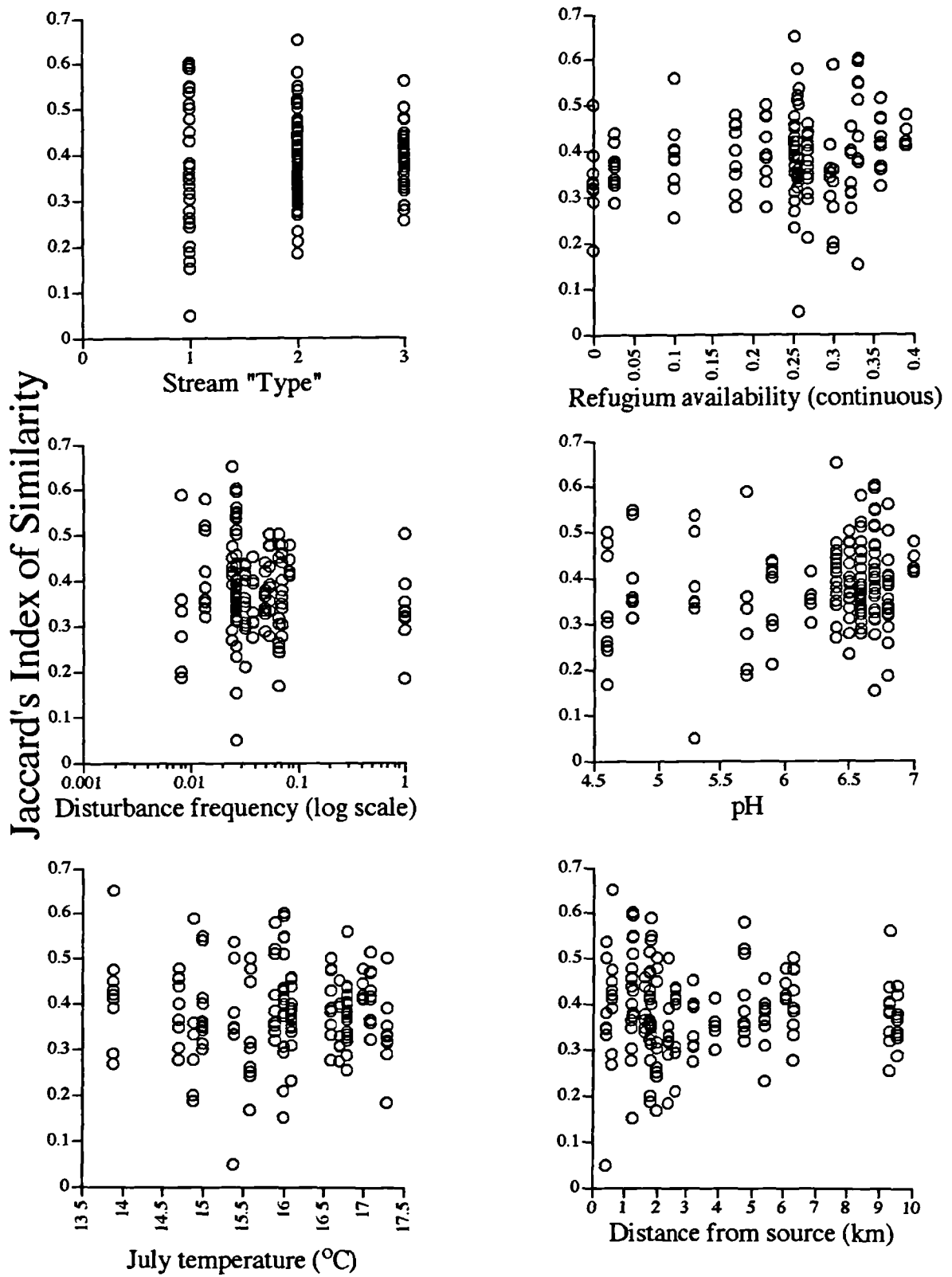
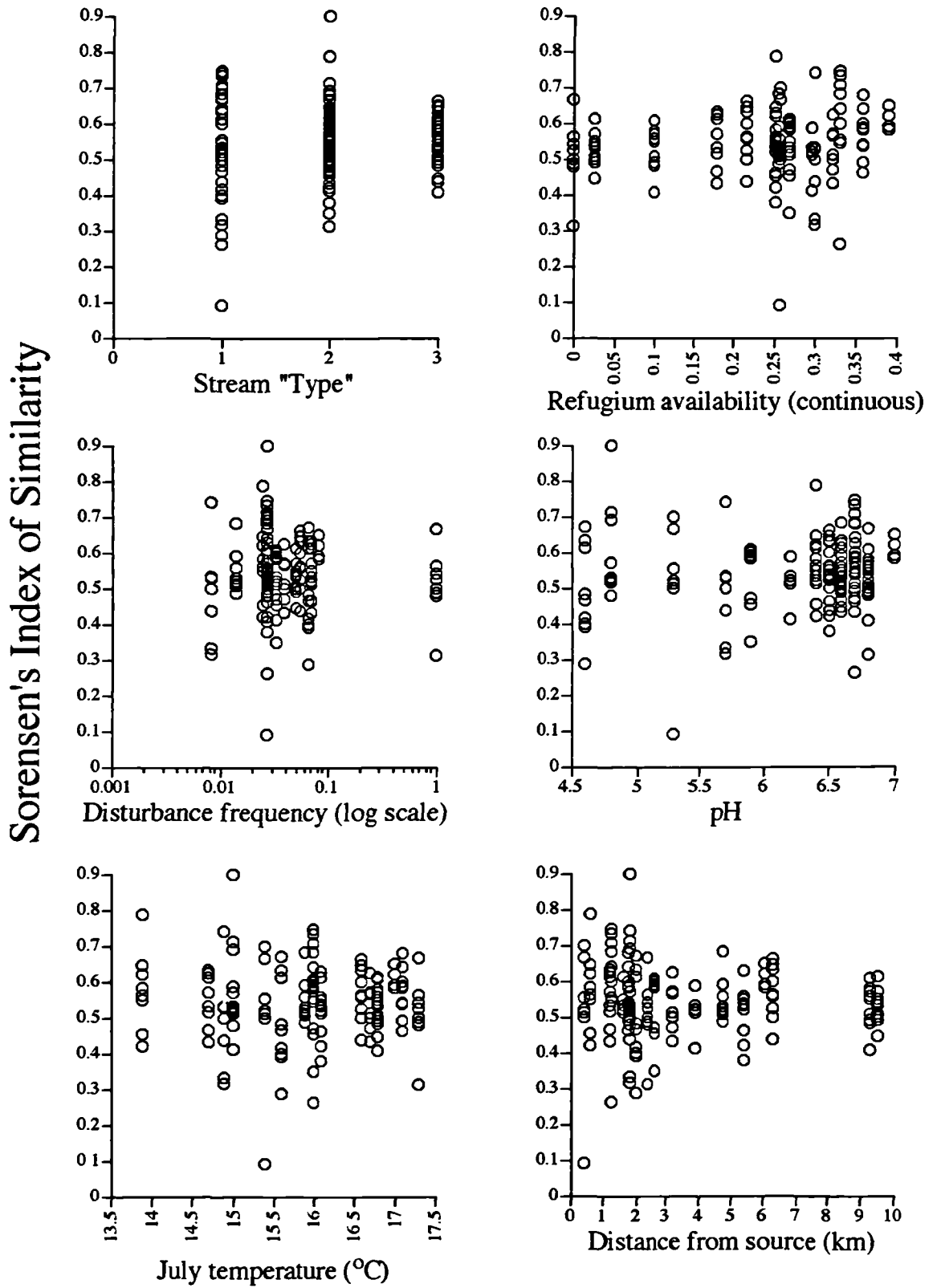


Fig. 5.5b.



Crowborough Warren. These were generally the sites that had been classified as being Type I streams (streams with a high refugia availability) and amongst the least disturbed streams. Amongst the streams with the least variance about the mean were Batt's Bridge, Marsh Green and Dodd's Bottom; the first two are classed as Type III streams, and both were amongst the most disturbed streams investigated. Dodd's Bottom is a Type II streams with an intermediate disturbance regime.

The persistence values in Figs. 5.1-5.4 are ordered according to time interval between samples. The column to the far left in each case (next to the mean) is thus the longest time interval (18 years between 1976 and 1994), the one next to it is 13 years, and time intervals then decline towards the right of the plot to include the spring-autumn comparisons (0.5 years). It might be expected that the longer time interval between comparisons would coincide with lower values of persistence, but no such pattern is apparent.

Townsend *et al* (1987) and Edmonds-Brown (1995) found a significant relationship between persistence and pH, distance from source and July temperature. Generally, cool, low pH upstream sites were more persistent than warmer circumneutral downstream sites. Although my data do not initially suggest any differences in persistence between sites, the indices were plotted against a number of environmental variables to test for a relationship. Variables were stream 'Type', continuous refugium availability, disturbance frequency, pH, July temperature and distance from source. All pairwise combinations of years at all sites were plotted on each graph simultaneously (Figs. 5.5a-b). No significant relationship was found between either persistence measure and any single environmental variable. This is perhaps not surprising since a pattern of persistence evident from comparing any two sets of samples may be confounded by plotting them along with other values. However, in a separate analysis, each set of pairwise comparisons (for example, the Jaccard's Indices for 1989-94 only for all sites) were plotted on their own against every environmental variable (results not shown). These more focused analyses also failed to show a significant relationship with any one environmental variable,

although the trend was towards higher persistence at cool, low pH upstream sites. This pattern has been more apparent in other years (Townsend *et al*, 1987).

5.3.ii Spearman's Index

Spearman's Rank Correlation Coefficient was calculated for all sites and all years. As mentioned previously, Spearman's Rank depends on n, the number of species present in both years. As the streams have very different species richnesses, Spearman's Rank will naturally vary between these sites. A high Spearman's Rank value in a species poor stream may be non-significant^{*}, whereas the same value in a species rich stream may be significant. A graphical presentation is therefore potentially confusing. Table 5.6 shows the combinations of years and streams where the Coefficient was significant. Withyham and Cackle Street were the most persistent sites, and neither Kidbrooke Park (ii) nor Lone Oak had a single significant Spearman's value. Lone Oak and Kidbrooke Park were also amongst the least persistent sites as calculated by Jaccard's and Sorensen's Indices. (The actual Jaccard's and Sorensen's values did not differ significantly between sites, but the variation between years within sites were greater for Lone Oak and Kidbrooke Park than many of the other sites).

Table 5.6 has been divided longitudinally to display the longest time interval between samples to the left (18 years) and the shortest to the right. The greatest number of streams found to be significantly persistent according to Spearman's rank was 8, and these were found in the ten and eight year intervals.

^{*} Significance was tested by comparing calculated coefficients to tabulated values (Zar, 1984).

Table 5. 6. Spearman's Rank Correlation Coefficient for all sites. ✓ indicates years that were significantly correlated.

	Autumn 1976-94	Autumn 1976-89	Autumn 1984-94	Autumn 1976-84	Autumn 1984-89	Autumn 1989-94	Spring 1990-94	Spring+ Autumn 1989-90	Spring+ Autumn 1994
Time interval (years)	18	13	10	8	5	5	4	0.5	0.5
Lavender Platt	✓	✓		✓			✓		
Weirwood Road								✓	
Kidbrooke Park (i)		✓							
Nutley Bridge	✓								
Old Lodge (i)		✓					✓		
Old Lodge (ii)	✓				✓	✓			✓
Crowborough Warren				✓					
Cackle Street		✓	✓	✓	✓	✓			
Dodd's Bottom	✓								
Fairwarp		✓		✓				✓	
Marden's Hill (i)			✓						
Marden's Hill (ii)		✓	✓						✓
Below Friar's Gate			✓						
Old Forge							✓		
Batt's Bridge				✓					
Maresfield		✓		✓		✓			
Marsh Green			✓		✓		✓		
Half Moon Inn									✓
Withyham	✓		✓	✓	✓	✓	✓	✓	
Withyham Green			✓	✓	✓				
Boringwheel Mill			✓						
Broadstone Stream					✓	✓			
Lone Oak									
Kidbrooke Park ii									

5.3.iii Multivariate analyses

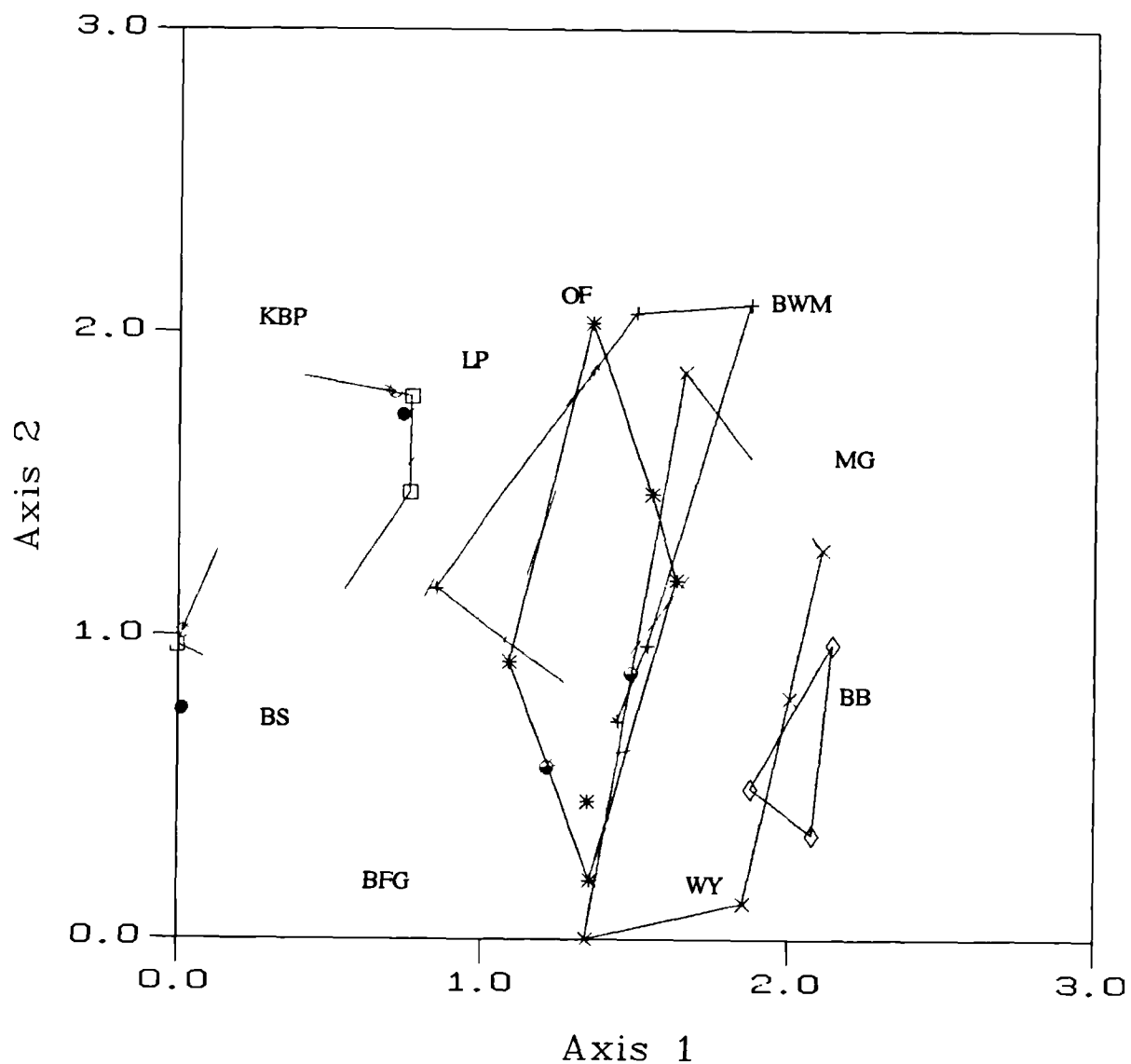
A DCA was performed on the raw data for all years. The data were $\ln(x+1)$ transformed to ensure a normal distribution, and rare species were down weighted. This option gives less weight to rare species in the analyses, and thus avoids distortion. The gradient length of Axis 1 was found to be 2.264 (Table 5.7) indicating good separation along the first axis by the unimodal model, so the DCA was used for further interpretation.

Table 5.7. Results of the DCA for species data for the six sampling occasions 1976-94, including both autumn and spring.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.262	0.176	0.088	0.068
Gradient length	2.264	1.584	1.728	1.608
Cumulative % variation	12.7	21.3	25.6	28.9
Sum of all unconstrained Eigenvalues				2.055

The Eigenvalues for Axis 1 and 2 were quite low, and only a small percent of the total variation (21.3%) was explained by the first two axes. However, low Eigenvalues are common with very large data sets (Ryves, pers. com.), and the biplot had a very high number of points on it which complicated the interpretation. To simplify the graphical representation nine sites were chosen that covered the whole range of pH, disturbance frequency, stream 'Types', etc. (Table 5.8). A DCA was performed, and the values were plotted (Table 5.9; Fig. 5.6). Eigenvalues were now higher, indicating a better separation along the first and second axes. Because the sum of all unconstrained Eigenvalues is now higher, the cumulative percent variation is actually lower since the cumulative percent variation is equal to the Eigenvalue of an axis divided by the sum of all unconstrained Eigenvalues.

Fig. 5.6. DCA biplot of the nine streams, all years, both seasons. Each cluster is a site, and the points within the clusters are sampling occasions (years). The tighter the cluster, the more similar are the years compared within the cluster, inferring higher persistence.



LP	Lavender Platt
KBP	Kidbrooke Park
BFG	Below Friar's Gate
OF	Old Forge
BB	Batt's Bridge
MG	Marsh Green
WY	Withyham
BWM	Boringwheel Mill
BS	Broadstone Stream

Table 5.8. The nine sites chosen as representative of the whole suite of sites for the multivariate biplot. The site initials are used in the biplot.

Site initials	Site name	Range of pH	Disturbance frequency	Stream "Type"	Distance from headwater (km)
BS	Broadstone Stream	4.0-6.2	0.0438	I	0.58
KBP	Kidbrooke Park (i)	4.3-6.1	0.0082	I	1.77
LP	Lavender Platt	4.5-6.0	0.0246	II	0.61
BFG	Below Friar's Gate	5.0-6.3	0.0273	II	5.41
OF	Old Forge	5.5-7.0	0.0383	II	3.19
BWM	Boringwheel Mill	5.3-7.1	1.0000	II	2.35
MG	Marsh Green	4.4-6.8	0.0493	III	9.54
WY	Withyham	5.4-6.7	0.0273	III	9.29
BB	Batt's Bridge	5.3-7.4	0.0821	III	6.05

Table 5.9. Results of DCA on nine streams, all years and seasons included.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.313	0.240	0.129	0.095
Gradient length	2.154	2.095	1.666	2.198
Cumulative % variation	11.0	19.5	24.0	27.3
Sum of all unconstrained Eigenvalues	2.846			

Points that are close to each other on biplots are the most similar, and vice versa. The clusters in Fig. 5.6 represent individual streams, and each point within a cluster represents a sampling occasion (year and season). The area a cluster covers is proportional to the variation found between the samples; the greater the area covered, the more variation between years. All sites varied greatly between years, and the variation between years in the same stream (spread within clusters) was greater than that between streams in the same years (close proximity between clusters). There was little difference in the variation between streams (cluster sizes about equal), although

✱ Although Batt's Bridge did not have significantly higher Jaccard's and Sorensen's values than any other site, the variation between years within the site was low. Multivariate analyses showed spring community assemblages to be very different from autumn assemblages in all streams, and the low variation in Batt's Bridge could also reflect that no samples were taken in the spring. When spring samples were omitted at all sites (Fig 5.8) Batt's Bridge did not appear to be any more persistent than the other sites. When omitting spring samples from the multivariate analyses, therefore, there was no difference in persistence between sites, a pattern also suggested by the similarity indices.

Batt's Bridge did vary less between years (clustered more tightly), suggesting a higher persistence.[★]

A CCA was performed to identify the importance of the environmental variables measured (Table 5.10; Fig. 5.7). Axis 1 was highly correlated with pH, July temperature and Type I streams, and Axis 2 with 1994 data and spring data. This means that pH, temperature and high refugium availability are highly correlated and

Table 5.10. Result of CCA of species data for nine streams only for all years and seasons.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.271	0.202	0.132	0.113
% variation of species data	13.1	22.9	29.3	34.8
Sum of all unconstrained Eigenvalues	2.063			
Sum of all canonical Eigenvalues	1.027			

(of the imposed variables) they explain most of the species variance (13.1%). 1994 and spring data were also important in explaining species variance (22.9-13.1=9.8%), but not as important as pH (discussed below). The results also showed that about 50% of the variation in species data was explained by the environmental variables; the sum of the canonical Eigenvalues were about half of the unconstrained Eigenvalues ($1.027/2.063 = 49.7\%$). The significance of the CCA results was verified with a Monte Carlo Permutation Test (99 permutations under full model, $p = 0.01$). To eliminate the effects of the very different species data in the 1994 and spring samples a DCA was run excluding these samples (Table 5.11; Fig. 5.8). The variation within sites was now reduced, a greater percentage of variation was explained by the first two axes (29.5%) but there was still very little difference in variation between sites.

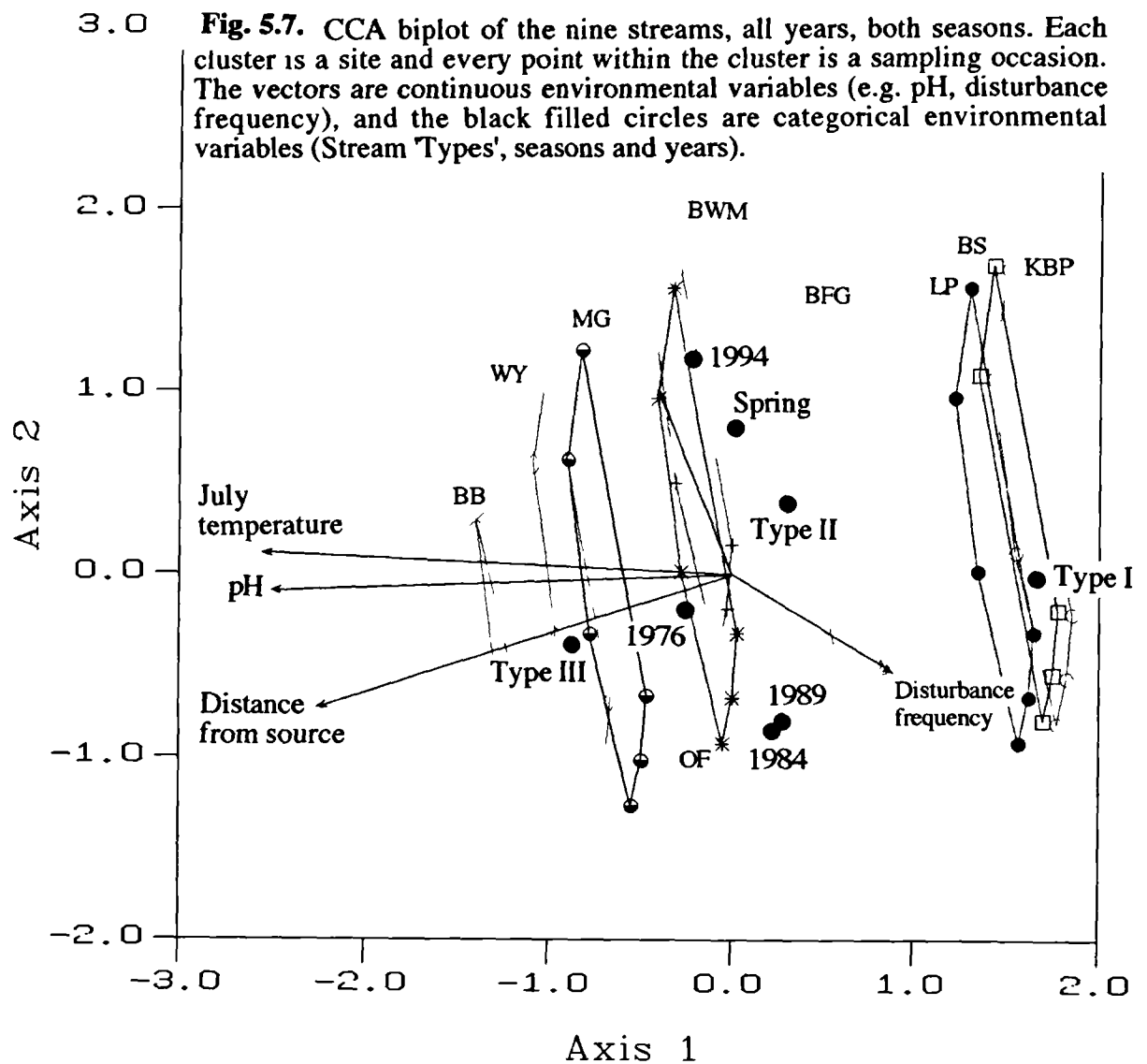


Fig. 5.8. DCA biplot of the nine streams for autumn, 1976-89 values only. Spring and 1994 samples were omitted as the CCA showed they influenced the species variance greatly.

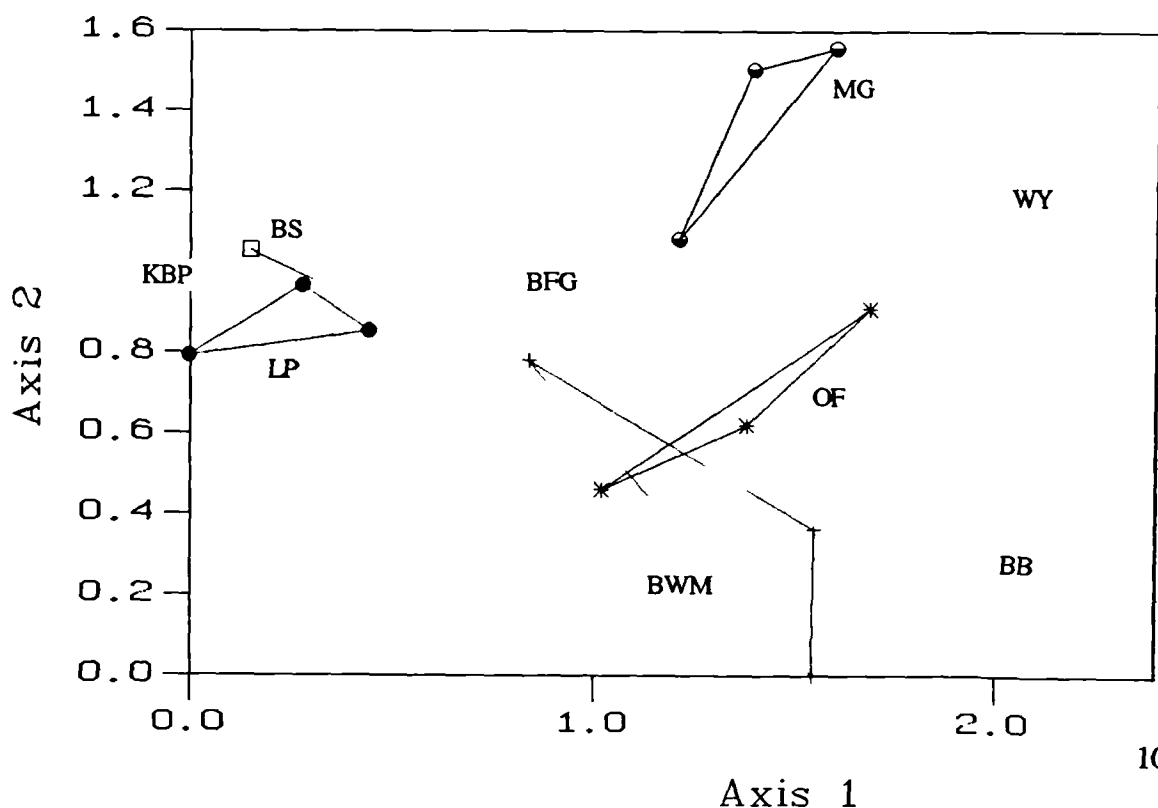


Table 5.11. Results of DCA of species data on nine streams, excluding 1994 and spring samples.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.337	0.135	0.76	0.049
Gradient length	2.073	1.558	1.773	1.335
Cumulative % variation	21.1	29.5	34.3	37.4
Sum of all unconstrained Eigenvalues				1.597

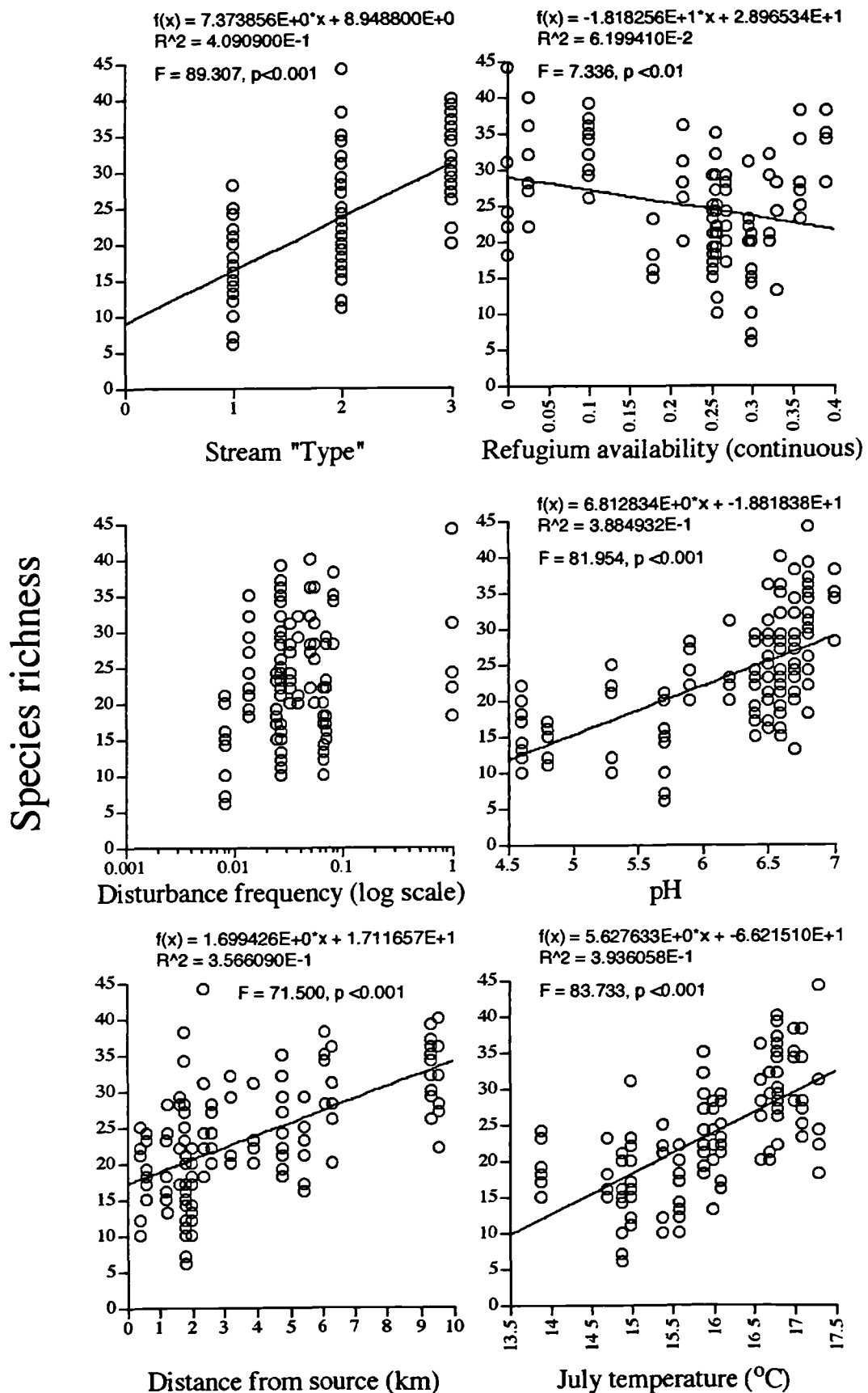
5.3.iv Species richness

The stepwise multiple regression of the species richness versus environmental data showed the best correlation with July temperature and distance from source (Table 5.12). A strong correlation was also found between pH, July temperature, stream 'Type' and distance from source. If pH and refugium availability were left out of the regression, the significance of the interaction between pH, July temperature, distance from source and stream 'Type' increased to 0.002 (Table 5.13). If linear regressions were made of species richness against each variable in turn, all were significantly correlated except for disturbance frequency (Fig. 5.9); it is clear that

Table 5.12. Results of stepwise multiple regression of species richness against environmental variables.

	Sum of Squares	Df	F-Ratio	P
July temperature	397.795	1	13.695	0.003
Distance from source	291.272	1	10.028	0.002
Refugia (continuous)	95.639	1	3.293	0.072
pH	110.917	1	3.819	0.053
pH*July temp*Type	235.476	2	4.054	0.020
*Distance source				
Squared multiple R =				0.521

Fig. 5.9. Regression of species richness against environmental variables. Total data set was plotted, i.e. all years and seasons at all sites. Disturbance frequency was plotted on a log scale, as the value for Boringwheel Mill was two orders of magnitude higher than for most other sites.



★

Boringwheel Mill had a disturbance frequency of 365 days per year (see Chapter 3). This high disturbance frequency was an artefact of the way disturbance was measured (by tracer particles) and was unique to this site. Although this site is believed to be more disturbed than all the other sites investigated, the exact disturbance frequency is uncertain and, therefore, throughout this thesis analyses have been done including and omitting the site to avoid this one disturbance value to bias the results.

★ ★

It was only possible to statistically test for between-site variations, not within-site variations. It was, therefore, only possible to confirm that no one site was more persistent than another, but it could not be statistically tested whether the within-site variations were greater in some sites than in others. All sites had low indices of similarity (means: Jaccard's = 0.39, Sorensen's = 0.54), indicating low persistence. The variation of the similarity indices did vary within sites, however (indicated by the standard deviations about the mean on the graphs). Thus, although Batt's Bridge had low persistence indices (like all other sites), the indices showed little variation between years.

Table 5.13. Stepwise multiple regression leaving out the effects of pH and refugium availability.

	Sum of Squares	Df	F-Ratio	P
July temperature	851.213	1	27.704	0.59 10 ⁻⁶
Distance from source	341.258	1	11.107	0.001
pH*July temp*Type	405.846	2	6.604	0.002
*Distance source				
Squared multiple R = 0.528				

many of the variables are highly inter-correlated.

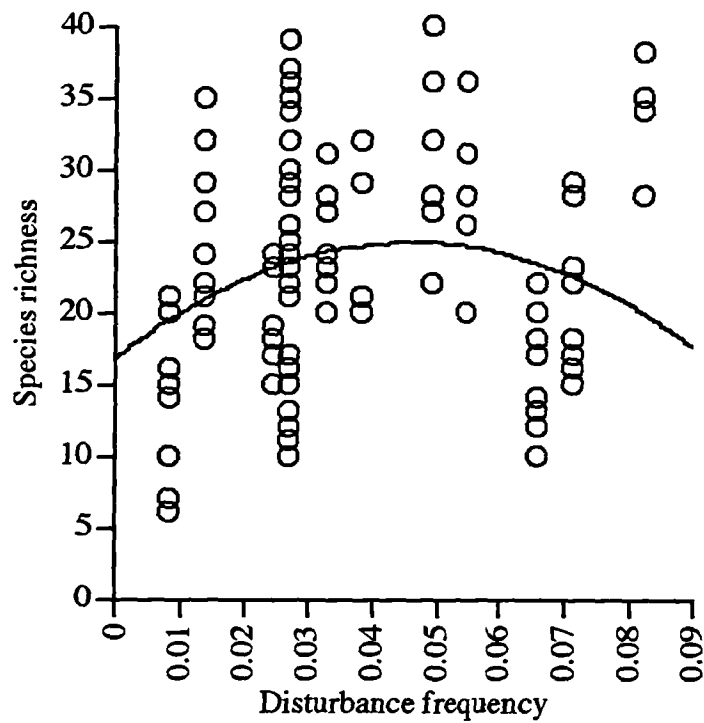
As mentioned in the introduction, species richness is expected to be highest at an intermediate disturbance level. As no linear relationship was found between species richness and disturbance frequency, a parabola was fitted to the data leaving out Boringwheel Mill as the very high disturbance frequency^{*} found at this site heavily influenced the results (Fig. 5.10). This fit was not statistically significant either, however (p=0.511).

5.4 Discussion

The three persistence indices gave similar results, but the fact that they could not be tested statistically makes them less valuable.^{**} The results of these methods can therefore only be descriptive and are often vague. Generally they suggested very few differences between sites. The low observed variation in index values between years at Batt's Bridge, however, was also reflected in the multivariate results.

The Detrended Correspondence Analysis (DCA) showed very little difference in variation between sites. All sites varied greatly, with the possible exception of Batt's Bridge. The spring (1990 and 1994) and 1994 data were very different from the data collected in the previous years. The difference found between the spring and autumn data is not unexpected, and can be explained by seasonal variations; communities are likely to vary more between spring and autumn in one year, than in

Fig. 5.10. Polynomial regression of species richness against disturbance frequency. Boringwheel Mill is left out, as the very high disturbance frequency found at this site heavily influences the analyses. The fit is not statistically significant.



the same season but years apart. The variance caused by the 1994 data can be explained by one of two factors; either there is a sampling error or the communities actually changed significantly in the five years since 1989. By coincidence, previous sampling occasions have followed unusually hot, dry summers (Edmonds-Brown, 1995), whereas the 1994 October sampling followed a summer with average temperature and precipitation. This might go some way to explain the differences in community composition in all streams in 1994. Furthermore, the 1994 pattern was similar for all sites and, when leaving out the spring (1990 and 1994) and 1994 data, there was still little difference between the streams with regards to variation in their respective communities.

It seems highly likely that the different community compositions seen in 1994 do reflect a genuine change in the stream communities in the Ashdown Forest, and changes in chemistry measured for the Acid Waters Monitoring Network (AWMN) support this view. The AWMN is a government funded project set up in 1988 to collect long-term chemical and biological data to facilitate the assessment of trends in surface water acidity. One of the 22 sites monitored by the AWMN in the UK is located in the Ashdown Forest (Old Lodge). Species have been observed, particularly in the more acidic sites, that were previously absent or scarce. Recent observations at Broadstone Stream, for example, have shown that high densities of *Cordulegaster boltonii*, the Golden ringed Dragonfly, have suddenly appeared (Hildrew, pers. comm.), and the addition of such a top predator is likely to influence the whole food web of the stream.

Species richness was found to be highest at sites with a relatively high July temperature, and further from source. Individual regressions also suggested that high pH streams with low refugium availability had higher species richness, although this was not shown in the stepwise regression. These results confirm the findings of Townsend *et al.* (1983), although pH was not found to be the overall important influencing variable. Many of these environmental variables strongly interact; thus the headwater streams close to the source are generally cooler, have lower pH, are

generally more 'flashy', and have a more heterogeneous flow, thus possibly providing more flow refugia.

No single variable solely determined species richness. Disturbance, as measured by tracer particle movements, did not influence species richness greatly, and the intermediate disturbance hypothesis was not reflected in the results; if anything, species richness increased with disturbance frequency. The intermediate disturbance hypothesis can, however, not be rejected. It is possible that this survey has only included sites that would normally be classed as being of low to medium disturbance, and that therefore no streams of high disturbance were measured. Thus, only half of the response model might have been tested (the 'increasing slope' of the parabola), as reflected by the increasing species richness.

Thus, a difference was found in community compositions between the 26 streams. There was no systematic difference in community persistence between streams, and little or no difference in variation within streams. This situation reflects that described in Table 5.1, example (c), and suggests that environmental variables are important in structuring the communities, and that species complement reflects the habitat available. It thus lends indirect support to Southwood's Habitat Templet Hypothesis. It should thus be possible to see differences in species traits that reflect these adaptations, and this will be addressed in Chapter 6.

CHAPTER 6: Species traits in relation to environmental variables.

6.1 Introduction

So far we have seen how the 26 streams investigated have different physical habitats with regards to disturbance frequency (Chapter 3) and refugium availability (Chapter 4). We have also seen how the benthic communities differ between streams and how this is primarily related to pH, July temperature and high refugium availability and, secondly, to disturbance frequency (Chapter 5); cool, low pH upstream sites in general have different community compositions to warmer, circumneutral downstream sites. These same upstream sites were also found to be less rich in species than the downstream sites. Although the communities are different, however, they are equally persistent and there is little or no consistent difference in persistence within sites. This suggests some degree of adaptation to the habitat, and lends circumstantial support to Southwood's Habitat Templet Hypothesis (1977, 1988), "The habitat provides the templet upon which evolution forges characteristic life-history strategies". Differences in these life-history strategies, or species traits, should be apparent between the streams investigated.

Southwood (1988) listed the main traits on which selection can act under five headings: (i) extent of investment in physiological adaptations to unfavourable physical conditions; (ii) extent of investment in defence; (iii) investment in food harvesting and somatic development; (iv) investment in reproductive activities; (v) investment in tactics for escape in time and space. Working with a spatio-temporal templet, emphasis is given to the final trait (v) in this thesis, as species can generally be said to escape temporal variations (disturbances) through the use of spatial variations (refugia).

Recently much research has investigated the link between the physical habitat and species traits (Townsend & Hildrew, 1994; Usseglio-Polatera, 1994; Robertson *et al*, 1997; Statzner *et al*, 1997; Townsend *et al*, 1997). Within a templet of spatio-

temporal variability some research has focused on a few specific traits (Robertson *et al*, 1997; Statzner *et al*, 1997) and some on resilience and resistance traits in general (Townsend & Hildrew, 1994; Townsend *et al*, 1997). Townsend & Hildrew's resistance/ resilience approach (1994) has been adopted by many workers.

The terms 'resilience' and 'resistance' describe situations in which assemblages persist unchanged (they show resistance) through a disturbance or return quickly to their pre-disturbance state (demonstrating resilience). Resistance traits include effective hold-fast mechanisms (such as hooks or suckers) and streamlining, flattening or flexible body forms that reduce the risk of the organism being dislodged. Rapid re-establishment of populations after a disturbance may occur either if reproductive growth is fast or if populations are very mobile and able to use potential refugia, either actively or passively. Resilience traits include reproductive characteristics such as a large number of eggs, a long oviposition period, egg attachment and laying more than one clutch. High mobility, either through drift, crawling or swimming, is also associated with resilience, aiding rapid recolonisation from potential refugia.

In highly variable habitats resilience/resistance traits are expected to dominate because only species with traits that permit success in the face of disturbance will survive. A mixture of traits may be expected in more 'stable' habitats (Townsend & Hildrew, 1994), firstly because constant conditions do not directly preclude organisms with traits more suited to variable environments and, secondly, because these organisms are not necessarily outcompeted by superior species. Although biotic interactions may be very important in some cases in 'stable' environments (e.g. Hemphill & Cooper, 1983; MacAuliffe, 1984; Lancaster, 1996), empirical evidence suggests that many lotic habitats are so dynamic that complete dominance by competitive species is unlikely.

Streams can be considered at a variety of spatial scales (Frissell, 1986), and one of the great problems in lotic ecology is choosing a scale that is appropriate to the organisms studied. Lotic communities are dominated by insects, which are small in

size, have a large number of offspring, short life cycles, etc. (the classic r-selected species of MacArthur & Wilson, 1967 and Pianka, 1970), and fish which are streamlined and very mobile. On an evolutionary time-scale, perhaps these general life history characteristics can be said to have been selected for life in the harsh environment of running water. On a smaller geographical scale, within and between streams, differences between traits may be more difficult to distinguish, as the organisms compared are generally all of a relatively small size, with short life cycles, etc.. Further, rather than evolutionary changes 'in situ' any differences in species traits between streams are likely to be due to differential recruitment from within a local pool of available species, with a limited range of species traits.

Furthermore, at this small scale the problem of trade-offs of species traits arises (Southwood, 1988; Townsend & Hildrew, 1994; Statzner *et al*, 1997). If a species has a particularly good hold-fast mechanism, for example, then it can 'afford' a large body size or to be non-mobile. There may, therefore, be several 'solutions' to the same evolutionary problem, and it becomes difficult to classify only one species as being more or less resistant or resilient than another. Thus, much of the research on this subject has been unable to identify distinct patterns in species traits (Usseglio-Polatera, 1994; Death, 1995; Robertson *et al*, 1997).

In this Chapter I compare the species traits of a large proportion of the species to the environmental variables of their habitats and, particularly, to the chosen axes of the Habitat Templet (disturbance frequency and refugium availability).

6.2 Methods

A list of species traits was drawn up from a literature review (Hynes, 1977; Elliott *et al*, 1988; Friday, 1988; Wallace *et al*, 1990; Usseglio-Polatera, 1994; Tachet *et al*, 1994; Usseglio-Polatera & Tachet, 1994; Richoux, 1994; Edington & Hildrew, 1995; Statzner *et al*, 1997; Townsend *et al*, 1997).

Detailed information on reproductive traits was not available for all species (Statzner *et al*, 1997), so the species x traits matrix is not complete. Ordination

techniques in CANOCO do not allow missing data, so the data set was divided into two; a 'morphology' file, with the complete species list but with a shortened list of (mainly) morphological traits that were known for all species, and a 'reproduction' file, with a shorter list of species but for each of which a good list of reproductive traits was available. Not all the traits available for species in the 'reproduction' file were included, because in CCA the list of traits cannot be longer than the list of species. To reduce the list of traits these morphological features that had already been tested in the 'morphology' file were not included. Traits were given binary coding.

Multivariate ordination was used to analyse the data. The use of multivariate statistics in CANOCO is discussed in detail in Chapter 5. Initially a DCA was performed on the complete species x site data from October 1994 on their own to discover any differences in community structure between sites. A CCA was then performed on the percentage composition data to discover which measured environmental variables explain most of this separation. Percentage data were used to eliminate the effect of abundance; circumneutral sites have been shown to have higher absolute numerical abundance than acid sites, but it is the species composition that is of interest here.

One way of relating traits to species or sites is essentially to use the trait data as the 'environmental' or 'predicting' variables. Thus, instead of species being separated out according to pH or disturbance frequency (for instance), the species variation can be explained by the traits. A CCA allows for the interchanging of species and samples (or traits and species) in the input data files, because weighted averaging methods treat species and samples in a symmetrical way (ter Braak, 1988). The species x site matrix was, therefore, entered as the species input file with species as objects and sites as variables (the opposite way to usual), and the species x traits matrix was entered as the environmental data file, with species as objects and traits as predictors. Long dialogue and forward selection were chosen, sample scores were 'weighted mean species' scores (not default 2), and rare species were not

downweighted, as in this case the 'species' were actually the sites. Monte Carlo Permutation tests were then run to test the validity of the analyses.

Forward selection in CCA tests one variable at a time; the first variable chosen explains the greatest part of the total variance and subsequent variables explain decreasingly less. At each stage a test was made for the best variable (code -999) and, if significant, it was included. Forward selection was stopped when no more variables significantly explained total variance, and 'unimportant' variables were thus omitted from the final analysis. Often, if two variables were highly correlated, they both came up equally important to start with. When either variable is selected, the other then loses importance, as that variable will contribute very little to explain the overall species variance.

6.3 Results

6.3.i Ordination of species x site data only - all sites

The gradient length of the first axis in the initial DCA was 2.048 (Table 6.1.), so either a unimodal or linear model could be used, and the DCA was chosen. Eigenvalues were 0.280 and 0.087 for Axis 1 and 2, respectively, and 33.6% of the variation in the species data was explained by the first two axes. These values, although not high, are in the normal range for ecological data (Ryves pers. com.).

Table 6.1. Results of the DCA for species data in all streams, October 1994. Data were $\ln(x+1)$ transformed and rare species downweighted.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.280	0.087	0.040	0.029
Gradient length	2.048	1.562	0.916	1.134
Cumulative % variation	25.6	33.6	37.3	40.0
Sum of all unconstrained Eigenvalues	1.092			

The closer two sites are to each other on an ordination biplot, the more similar their community compositions are. The biplot (Fig. 6.1) showed a separation of sites, indicating a real difference in community composition between sites.

6.3.ii Ordination of species x site matrix constrained by environmental variables

A CCA was then performed on the percentage composition data to see which environmental variables explained most of the separation. Due to missing environmental data (Chapter 3) Weirwood Road, Maresfield and Withyham Green were omitted. Distance from source and Type III streams were highly correlated (0.842, Table 6.2), indicating that downstream sites generally had lower refugium

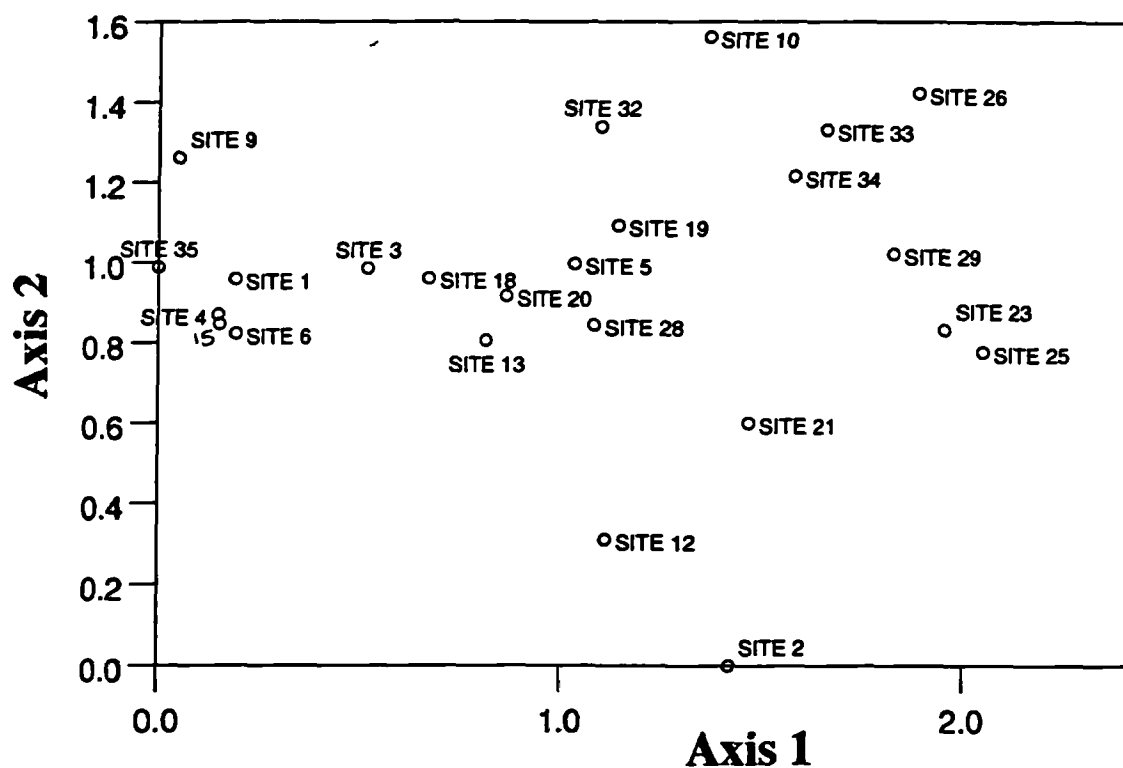
Table 6.2. Pearson's Matrix of Correlation between environmental variables. Due to missing environmental data Weirwood Road, Withyham Green and Maresfield were omitted.

	Type I	Type II	Type III	disturb.	pH	July °C	distance
				freq.			source
Type I	1						
Type II	-0.545	1					
Type III	-0.305	-0.632	1				
disturbance frequency	-0.162	0.225	-0.105	1			
pH	-0.669	0.152	0.445	0.248	1		
July temperature	-0.368	-0.204	0.572	0.386	<u>0.573</u>	1	
distance from source	-0.475	-0.354	<u>0.842</u>	-0.126	0.527	0.632	1
refugia	0.339	0.060	-0.382	-0.535	-0.296	-0.394	-0.467

availability. July temperature and pH were also highly correlated (0.573) and explained most of the separation along Axis 1 (Fig. 6.2.). Type I, II and III streams are shown as points rather than vectors on the biplot because they are not continuous variables, and were entered as 'Dummy variables' (binary coding). The longer the vector, the more important that variable is in explaining species variance, and the

Of the original 26 stream sites investigated, Old Lodge ii and Hendall were not included in this analysis. Field work at Hendall was discontinued at an early stage due to difficulty of access and lack of suitable riffle sections. Old Lodge ii was not sampled in October, 1994. This site was close to Old Lodge i (tens of metres), the invertebrate communities were assumed to be similar, and it was excluded to save time in the laboratory.

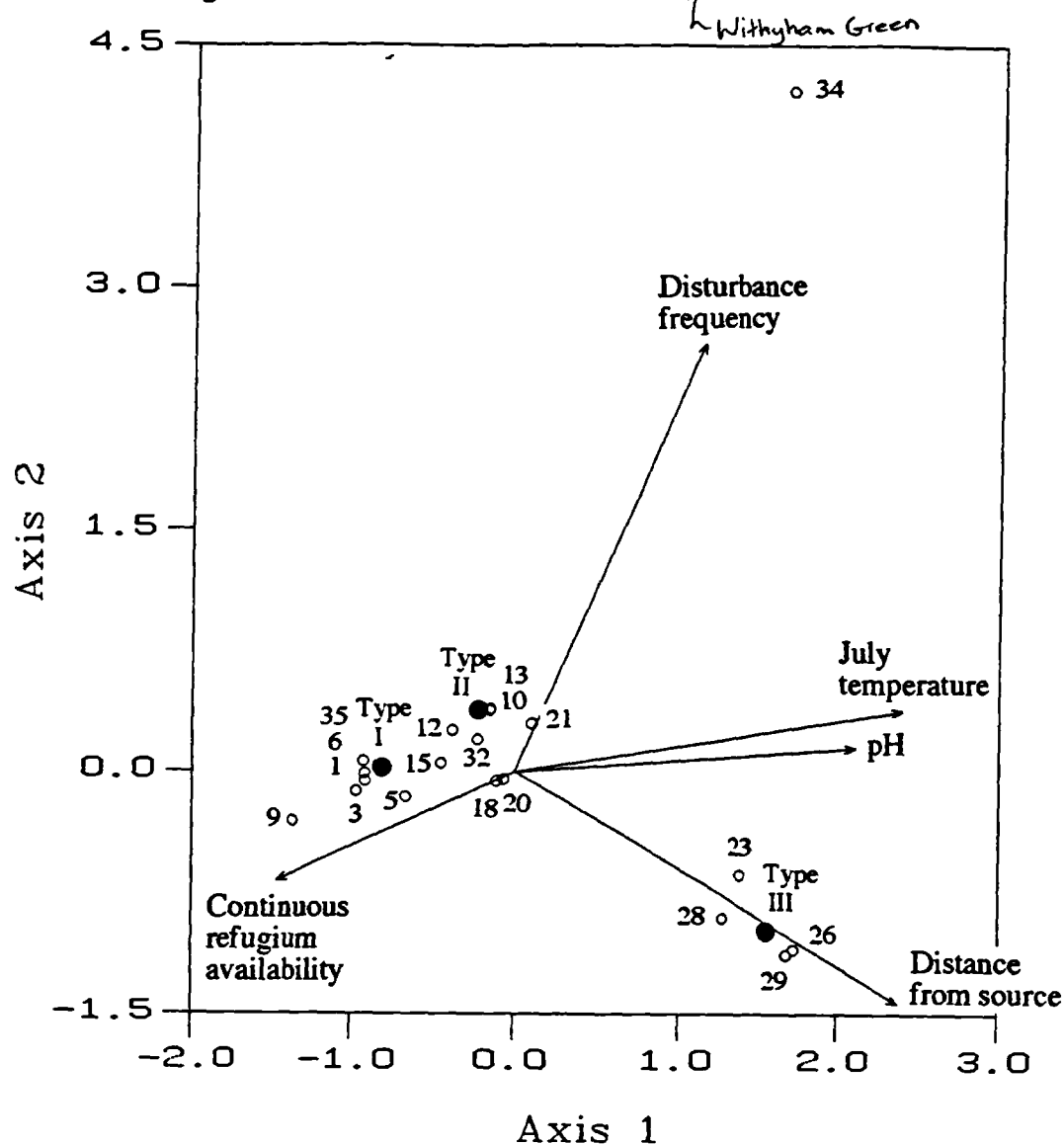
Fig. 6.1. Ordination biplot of the DCA results for species data in 24 streams, ⁵⁰¹October 1994. Data were $\ln(x+1)$ transformed and rare species were downweighted.



Site number	Site name	pH range	Site number	Site name	pH range
1	Lavender Platt	4.5-6.0	20	Below Friar's Gate	5.0-6.3
2	Weirwood Road	5.6-6.8	21	Old Forge	5.5-7.0
3	Kidbrooke Park (i)	4.3-6.1	23	Batt's Bridge	5.3-7.4
4	Kidbrooke Park (ii)	4.1-5.7	25	Maresfield	6.4-7.8
5	Nutley Bridge	4.4-6.8	26	Marsh Green	4.4-6.8
6	Old Lodge (i)	3.6-5.6	28	Half Moon Inn	5.1-7.0
9	Lone Oak	3.8-5.7	29	Withyham	5.4-6.7
10	Crowborough Warren	5.4-6.5	32	Clockhouse Lane	4.5-6.0
12	Cackle Street	5.1-6.8	33	Withyham Green	5.4-7.0
13	Dodd's Bottom	4.1-6.4	34	Boringwheel Mill	5.3-7.1
18	Marden's Hill (i)	5.0-6.3	35	Broadstone Stream	4.0-6.2
19	Marden's Hill (ii)	4.6-6.5	15	Fairwarp	5.5-6.9

The physical variables were identical within Kidbrooke Park i & ii and Marden's Hill i & ii, and therefore only the data from Kidbrooke Park i and Marden's Hill i were used in the analysis. With the omission of Weirwood Road, Withyham Green and Maresfield this left 19 sites in this analysis.

Fig. 6.2. Ordination biplot of the CCA results for species and environmental variables. Data were percentage transformed and rare species were downweighted. Due to missing environmental data Weirwood Road and Maresfield were omitted.



Site number	Site name	pH range	Site number	Site name	pH range
1	Lavender Platt	4.5-6.0	20	Below Friar's Gate	5.0-6.3
3	Kidbrooke Park	4.3-6.1	21	Old Forge	5.5-7.0
5	Nutley Bridge	4.4-6.8	23	Batt's Bridge	5.3-7.4
6	Old Lodge	3.6-5.6	26	Marsh Green	4.4-6.8
9	Lone Oak	3.8-5.7	28	Half Moon Inn	5.1-7.0
10	Crowborough Warren	5.4-6.5	29	Withyham	5.4-6.7
12	Cackle Street	5.1-6.8	32	Clockhouse Lane	4.5-6.0
13	Dodd's Bottom	4.1-6.4			
15	Fairwarp	5.5-6.9	34	Boringwheel Mill	5.3-7.1
18	Marden's Hill	4.6-6.5	35	Broadstone Stream	4.0-6.2

closer a site is to the tip of a vector, the stronger that vector explains variance in that site. The pH vector is strongly correlated with Axis 1, so sites negatively correlated with this vector (to the far left of the biplot) are the low pH sites (Broadstone, Lone Oak, Kidbrooke Park). The presence of 'outliers' along one environmental gradient may assign greater value to that gradient than if no 'outliers' were found. This explains why disturbance frequency was so highly correlated with Axis 2; Boringwheel Mill strongly influenced this gradient. The Eigenvalues were high, indicating good separation along the axes (Table 6.3), and the environmental variables measured explain 53% of the total variance (1.486/2.782). Forward selection showed 'Type III'

Table 6.3. Result of CCA of species and environmental variables. Due to missing environmental data Weirwood Road, Withyham Green and Maresfield were omitted.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.571	0.365	0.243	0.180
Cum. % variation of species data	18.6	31.7	40.4	46.9
Sum of all unconstrained Eigenvalues				2.782
Sum of all canonical Eigenvalues				1.486
Monte Carlo (99 unrestricted permutations under full model)	1st Axis: Overall: p=0.14	Overall: p=0.01		

and disturbance to be significant in explaining species variance; other variables did not contribute significantly in explaining species variance. 'Type III' was highly correlated with distance from source (0.842) and July temperature (0.572), and any one of these three variables would have been significant if chosen first in forward selection. Type I and the continuous measure of refugium availability were also very closely correlated, and both were strongly negatively correlated with distance from source and Type III.

The analysis was repeated leaving out Boringwheel Mill, as the disturbance frequency for this site was an order of magnitude higher than most of the other sites,

and it was therefore likely to influence the analyses disproportionately. Eigenvalues were slightly lower than when Boringwheel Mill was included, but about the same percentage variation was explained by the first two axes (Table 6.4). The biplot shows

Table 6.4. Result of CCA of species and environmental variables without Boringwheel Mill. Due to missing environmental data Weirwood Road, Withyham Green and Maresfield were also left out.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.513	0.256	0.226	0.134
Cum. % variation of species data	20.9	31.3	40.5	46.0
Sum of all unconstrained Eigenvalues				2.453
Sum of all canonical Eigenvalues				1.257
Monte Carlo (99 unrestricted permutations under full model)	1st Axis: Overall: p=0.08	Overall: p=0.02		

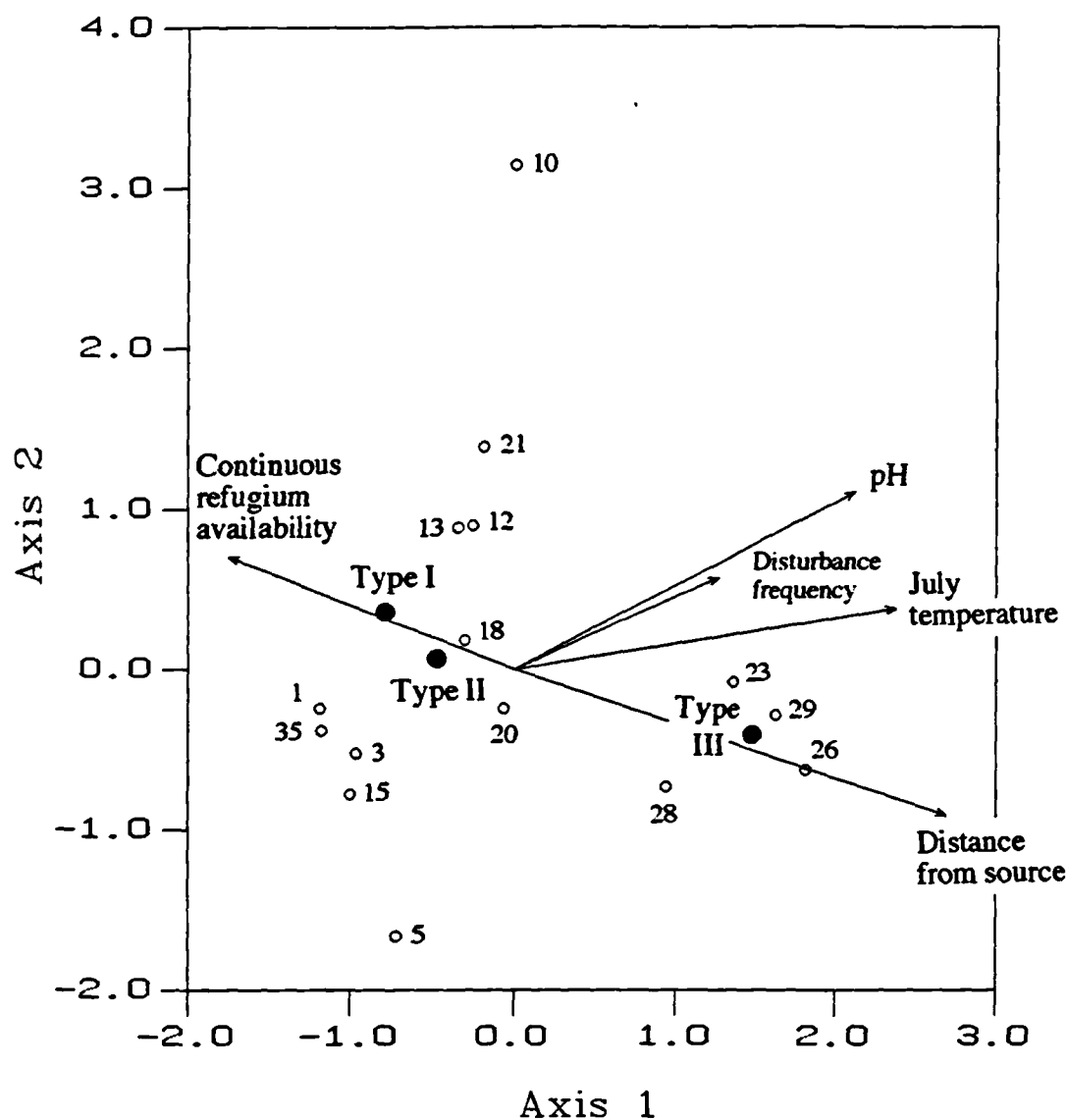
the difference in much better detail (Fig. 6.3). Type III, distance from source and July temperature are now most strongly correlated with the first axis, but no single environmental variable is correlated with the second axis. Disturbance has become less important; the vector is shorter. Forward selection showed that now only 'Type III' significantly explained species variance; disturbance frequency no longer contributes significantly.

Comparing the results of the CCAs performed with and without Boringwheel Mill it is clear that this outlier on the disturbance gradient strongly influences the analysis. Although care should be taken when including it in direct gradient analysis, it can be safely included in indirect gradient analysis where environmental variables are not imposed on the analysis.

A CCA was performed with pH, distance from source, continuous refugium availability and July temperature as covariables. This type of analysis is sometimes called a Partial CCA. The use of covariables allows the effect of specific variables to

Fig. 6.3. Ordination biplot of the CCA results for species and environmental variables excluding Boringwheel Mill. Data were percentage transformed and rare species were downweighted. Due to missing environmental data Weirwood Road and Maresfield were omitted, leaving 18 sites

Withyham Green



Site number	Site name	pH range	Site number	Site name	pH range
1	Lavender Platt	4.5-6.0	20	Below Friar's Gate	5.0-6.3
3	Kidbrooke Park	4.3-6.1	21	Old Forge	5.5-7.0
5	Nutley Bridge	4.4-6.8	23	Batt's Bridge	5.3-7.4
6	Old Lodge	3.6-5.6	26	Marsh Green	4.4-6.8
9	Lone Oak	3.8-5.7	28	Half Moon Inn	5.1-7.0
10	Crowborough Warren	5.4-6.5	29	Withyham	5.4-6.7
12	Cackle Street	5.1-6.8	32	Clockhouse Lane	4.5-6.0
13	Dodd's Bottom	4.1-6.4			
15	Fairwarp	5.5-6.9			
18	Marden's Hill	4.6-6.5	35	Broadstone Stream	4.0-6.2

be seen; in this case all but disturbance frequency and stream 'Types' (the Templet Axis variables) were entered as covariables. Boringwheel Mill was again not included in the analysis. The Eigenvalues were greatly reduced (Table 6.5), and only

Table 6.5. CCA on percentage transformed data with pH, distance from source, continuous refugium availability and July temperature as covariables. Rare species were downweighted.

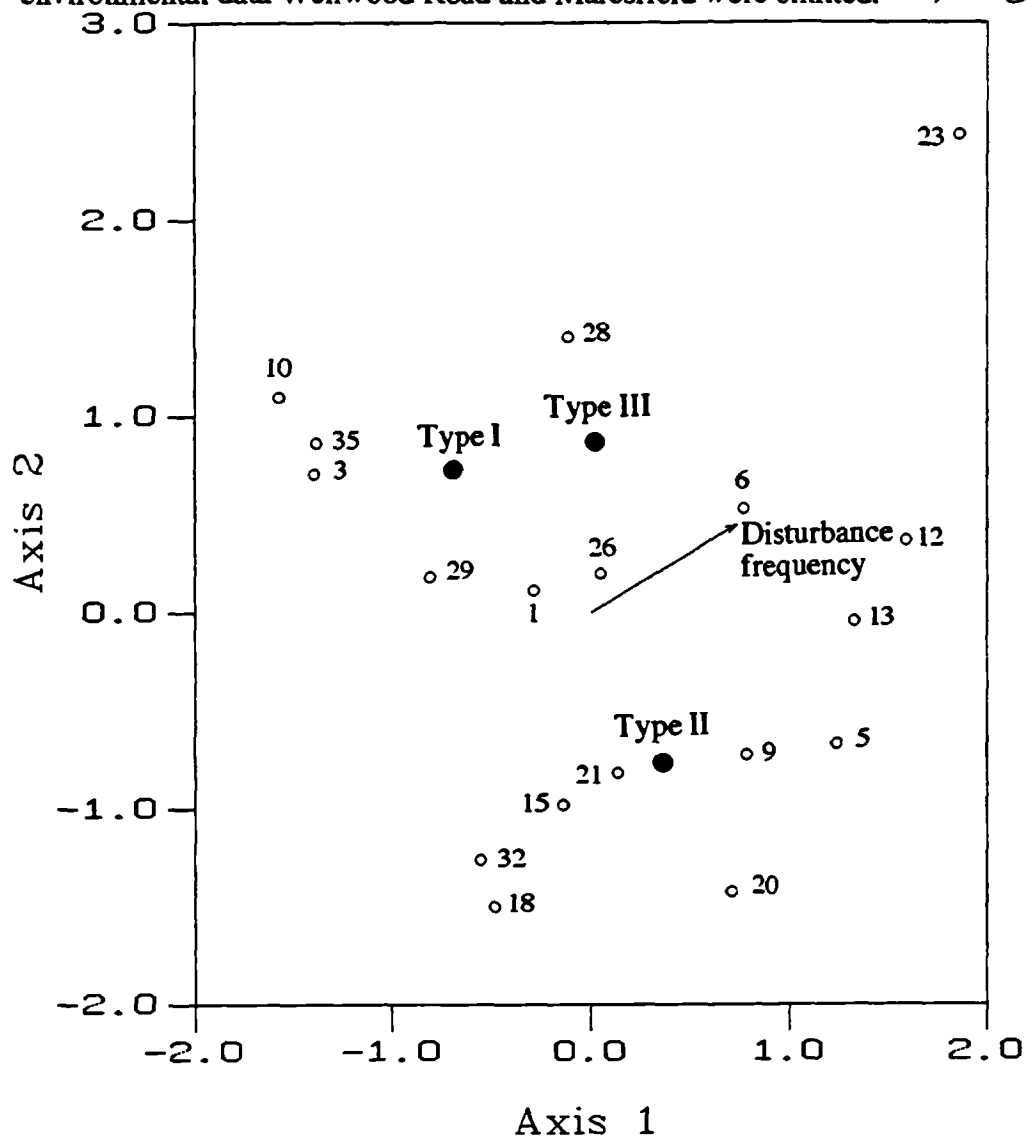
	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.141	0.096	0.063	0.359
Cum. % variation of species data	8.4	14.1	17.9	39.2
Sum of all unconstrained Eigenvalues				1.686
Sum of all canonical Eigenvalues				0.301
Monte Carlo (99 unrestricted permutations under full model)	1st Axis: Overall: p=0.70 p=0.55			

14.1% of the variation in the species data was explained by the first two axes. As only the first three axes are constrained, the Eigenvalues for the fourth axis is much higher than the first three; this and further axes are not constrained, and thus species variance beyond the third axis is explained by 'latent' (hypothetical) variables, not by measured environmental variables. Monte Carlo permutation tests showed that these three variables do not uniquely significantly explain species variance ($p > 0.05$), but that other variables are more important in explaining species variance. Although they do not solely explain species variance, it is still possible that they may be significant in a broader context in conjunction with other variables. The resulting biplot (Fig. 6.4) is thus a habitat templet on which streams are placed according to disturbance frequency and refugium availability (as measured by stream 'Types').

6.3.iii Ordination of species x sites, constrained by traits

Species traits, species, and the species x traits matrix are shown in Tables 6.6, 6.7 and Appendix 2, respectively. CCAs were run in which species x sites and species

Fig. 6.4. Ordination biplot of the CCA results for species and environmental variables excluding Boringwheel Mill. Distance from source, pH, continuous refugium availability and July temperature were entered as Covariables. Data were percentage transformed and rare species were downweighted. Due to missing environmental data Weirwood Road* and Maresfield were omitted. *, Withyham Green



Site number	Site name	pH range	Site number	Site name	pH range
1	Lavender Platt	4.5-6.0	20	Below Friar's Gate	5.0-6.3
3	Kidbrooke Park	4.3-6.1	21	Old Forge	5.5-7.0
5	Nutley Bridge	4.4-6.8	23	Batt's Bridge	5.3-7.4
6	Old Lodge	3.6-5.6	26	Marsh Green	4.4-6.8
9	Lone Oak	3.8-5.7	28	Half Moon Inn	5.1-7.0
10	Crowborough Warren	5.4-6.5	29	Withyham	5.4-6.7
12	Cackle Street	5.1-6.8	32	Clockhouse Lane	4.5-6.0
13	Dodd's Bottom	4.1-6.4			
15	Fairwarp	5.5-6.9			
18	Marden's Hill	4.6-6.5	35	Broadstone Stream	4.0-6.2

Table 6.6. Species traits (plus their letters used as labels in Appendix 2) for the invertebrates listed in Table 6.7.

Number	Species trait	
a1	Body size	large ($\geq 10\text{mm}$)
a2		small ($< 10\text{mm}$)
b1	Generations per year	(≤ 1)
b2		(> 1)
c1	Reproductive cycles per year	(≤ 1)
c2		(> 1)
d1	Incubation time	(≤ 4 weeks)
d2		(> 4 weeks)
e1	Egg attachment	none
e2		yes
f1	Clutch number	(1)
f2		(≥ 2)
g1	Egg number	few (≤ 500)
g2		many (> 500)
h1	Clutch structure	single/grouped
h2		egg mass
j1	Oviposition period	(≤ 2 months)
j2		(> 2 months)
k1	Body shape	streamlined
k2		flattened
k3		cylindrical
k4		spherical
m1	Body flexible?	yes
m2		no
n1	Locomotion	swimmers
n2		swimmers as adults
n3		crawlers
n4		crawlers as adults
n5		burrowers
n6		sedentary
n7		clingers
p1	dispersal	good
p2		poor
r1	case?	net-builder
r2		yes: plants/stones

Table 6.7. Families and species (plus codes) with available information on species traits.

DIPTERA		EPHEMEROPTERA	
chi	Chironomidae	epd	<i>Ephemera danica</i> Muller
	Simuliidae	epi	<i>Ephemerella ignita</i> (Poda)
sim	<i>Simulium</i> spp.	bae	<i>Baetis</i> spp.
cer	Ceratopogonidae	cae	<i>Caenis</i> spp.
	Tipulidae	lep	Leptophlebiidae
tip	<i>Tipula</i> spp.	haf	<i>Habrophlebia fusca</i> (Curtis)
ped	<i>Pedicia</i> spp.	pas	<i>Paraleptophlebia submarginata</i> (Stephens)
dic	<i>Dicranota</i> spp.	hep	Heptageniidae
dix	Dixidae	hes	<i>Heptagenia sulphurea</i> Muller
	Rhagionidae	rhs	<i>Rhithrogena semicolorata</i> (Curtis)
atx	<i>Atherix</i> spp.	ecd	<i>Ecdyonurus</i> spp.
PLECOPTERA		COLEOPTERA	
nem	Nemouridae		Hydrophilidae
	Leuctridae	hyc	<i>Hydrochara caraboides</i> (L.)
leu	<i>Leuctra</i> spp.	ber	<i>Berosus</i> spp.
	Chloroperlidae		Hydraenidae
sit	<i>Siphonoperla torrentium</i> Pictet	hyd	<i>Hydraena</i> spp.
	Perlodidae	lib	<i>Limnebius</i> spp.
isg	<i>Isoperla grammatica</i> (Poda)		Elmidae
	Capniidae	ela	<i>Elmis aenea</i> (Müller)
cab	<i>Capnia bifrons</i> (Newman)	liv	<i>Limnius volckmari</i> (Panzer)
		out	<i>Oulimnius tuberculatus</i> (Müller)
	TRICHOPTERA	stc	<i>Stenelmis canaliculata</i> (Gyllenhal)
	Polycentropodidae		Dytiscidae
plc	<i>Plectrocnemia conspersa</i> (Curtis)	agc	<i>Agabus chalconatus</i> (Panzer)
pol	<i>Polycentropus</i> spp.	cof	<i>Colymbetes fuscus</i> (L.)
	Psychomyiidae		Gyrinidae
tin	<i>Tinodes</i> spp.	orv	<i>Orechiochilus villosus</i> (Müller)
lyp	<i>Lype</i> spp.		ODONATA
	Philopotamidae	cob	<i>Cordulegaster boltonii</i> (Donovan)
phm	<i>Philopotamus montanus</i> (Donovan)		MEGALOPTERA
	Rhyacophilidae	sif	<i>Sialis fuliginosa</i> Pictet
rhd	<i>Rhyacophila dorsalis</i> (Curtis)		MOLLUSCA
	Glossosomatidae	anf	<i>Ancylus fluviatilis</i> (Müller)
agf	<i>Agapetus fuscipes</i> Curtis	bit	<i>Bithynia</i> spp.
	Hydropsychidae	pis	<i>Pisidium</i> spp.
hys	<i>Hydropsyche</i> spp.	lym	<i>Lymnaea</i> spp.
lim	Limnephilidae		MALACOSTRACA
cha	<i>Chaetopteryx</i> spp.	gap	<i>Gammarus pulex</i> (L.)
dra	<i>Drusus annulatus</i> (Stephens)	nia	<i>Niphargus aquilex</i> Schiodte
pot	<i>Potamophylax</i> spp.	ase	<i>Asellus</i> spp.
ste	<i>Stenophylax</i> spp.		OSTRACODA
	Sericostomatidae	ost	
stp	<i>Sericostoma personatum</i> (Spence)	hya	HYDRACARINA
	Leptoceridae		ANNELIDA
ath	<i>Athripsodes</i> spp.	oli	Oligochaetae
mys	<i>Mystacides</i> spp.	hir	Hirudinea
oec	<i>Oecetis</i> spp.		PLATYHELMINTHES
	Brachycentridae	pla	
brs	<i>Brachycentrus subnubilus</i> Curtis		
	Beraeidae		
bem	<i>Beraeodes minutus</i> (L.)		
	Goeridae		
sil	<i>Silo</i> spp.		
	Lepidostomatidae		
leh	<i>Lepidostoma hirtum</i> (Fabricius)		

* All traits were treated separately by the analysis, and these two significant traits are not always exhibited in the same species together. Thus, a species with a short incubation time does not necessarily also have few reproductive cycles per year. Short incubation time (d1) is considered to be 4 weeks or less, and few reproductive cycles (c1) is 1 or less per year (Table 6.6).

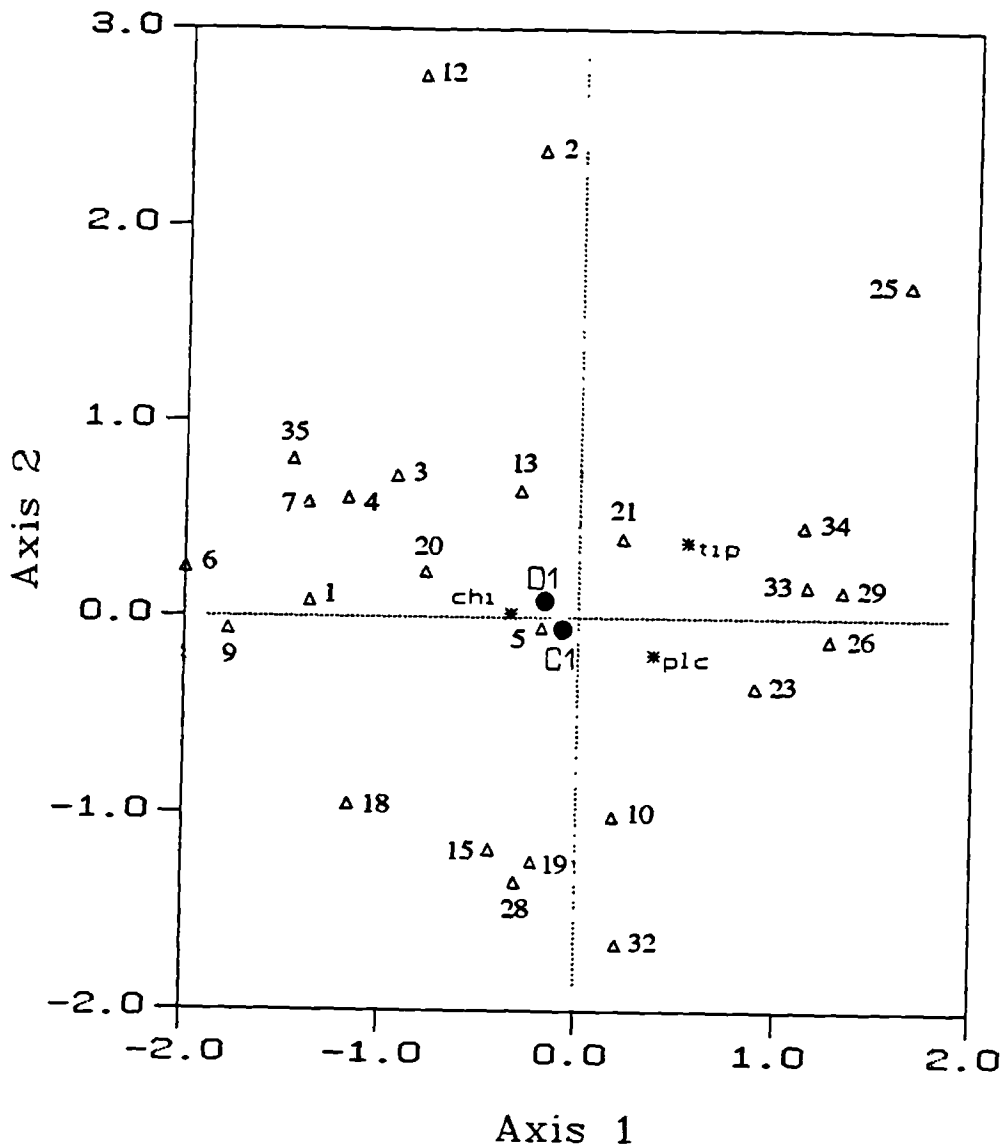
x traits were interchanged and traits were forwardly selected. Forward selection in the CCA for reproductive traits showed that only two traits significantly explained the variance: short incubation time (d1) and few reproductive cycles per year (c1)*. Axis 1 and 2 (along which the traits are arranged) explained 17.8% of the variation of the species data (Table 6.8). Fig. 6.5 shows the relation of species with these traits to the

Table 6.8. CCA for reproductive traits using forward selection.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.154	0.030	0.213	0.155
Cum. % variation of species data	14.8	17.8	38.4	53.3
Sum of all unconstrained Eigenvalues				1.035
Sum of all canonical Eigenvalues				0.184
Monte Carlo (99 unrestricted permutations under full model)	1st Axis: Overall: p=0.01	Overall: p=0.01		

sites in which they are found. Traits are shown as points rather than vectors because the data were binary, not continuous. The points can be interpreted in much the same way as vectors; they start in the origin (0;0) and the further away they are from the origin, the more important the variable is (this is the equivalent to long vectors). In Fig. 6.5 sites towards the top left of the biplot are positively correlated with d1, and sites towards the bottom left are positively correlated with c1. There are four possible combinations of these two traits that species can have; neither d1 or c1, both d1 and c1, or only one or the other. Only three of these combinations are actually found; no species had neither trait. Species with each combination of traits are shown on the graph with a star symbol. *Plectrocnemia conspersa*, for example, is shown as an example of a taxon with a long incubation time (d2) and few reproductive cycles per year (c1) (see legend for other combinations). There are only three points, as only three combinations of traits were found.

Fig. 6.5. Ordination biplot of the CCA results for reproductive traits in all streams. Data were $\ln(x+1)$ transformed and forward selection was used. Sites are represented by triangles and traits are black filled circles (D1 = short incubation time, C1 = few reproductive cycles per year). Star symbols are taxa that exhibit each of the three combinations of traits (see text for further explanation). The three taxa: Chironomidae (chi) (C1+D1), *Plectrocnemia conspersa* (plc) (C1+D2) and Tipulidae (tip) (C2+D1) are examples of taxa found in each group. For site names see Fig. 6.1.



Forward selection in the second CCA for the morphological traits significantly included two traits: non-flexible body (m2) and poor dispersal (p2). Only 9.5% of the variation in species data was explained by these two traits (Table 6.9), and the Eigenvalues were very low (0.094 and 0.029 for Axis 1 and 2, respectively), indicating poor separation along the axes. Overall, however, the two traits explained some variation in species significantly (Monte Carlo, $p = 0.01$). All four combinations

Table 6.9. CCA morphology traits only for all species, with forward selection.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.094	0.029	0.225	0.134
Cum. % variation of species data	7.2	9.5	26.9	37.3
Sum of all unconstrained Eigenvalues				1.296
Sum of all canonical Eigenvalues				0.123
Monte Carlo (99 unrestricted permutations under full model)	1st Axis: Overall: $p = 0.01$ $p = 0.01$			

of traits were found in the species (Fig. 6.6). Weirwood Road and Cackle Street were strongly negatively correlated with p2, suggesting that these two sites had a high proportion of species with good dispersal abilities.

If a CCA was performed on all the morphology traits without forward selection, the Eigenvalues and percent variance explained were higher, but overall the analysis was non-significant (Monte Carlo: $p=0.33$). A biplot of all the morphology traits is shown in Fig. 6.7. The traits are highly clustered and are not associated with either axis significantly.

The analyses of the species trait data suggested that, in general, no single trait successfully explained the distribution of species among sites or, in other words, very little differences in traits were found between sites with differing environmental variables. Although two traits significantly contributed to explain species variance in each CCA, Eigenvalues were very low and only 9.5% and 17.8% of species variation

Fig. 6.6. Ordination biplot of the CCA results for morphology traits in all streams. Data were $\ln(x+1)$ transformed and forward selection was used. Sites are represented by triangles and traits are black filled circles (M2 = body not flexible, P2 = poor dispersal). Star symbols are taxa that exhibit each of the four combinations of traits (see text for further explanation). The four taxa: Chironomidae (chi) (M1+P1), Ceratopogonidae (cer) (M1+P2), *Gammarus pulex* (gap) (M2+P1) and Tipulidae (tip) (M2+P2) are examples of taxa found in each group. For site names see Fig. 6.1.

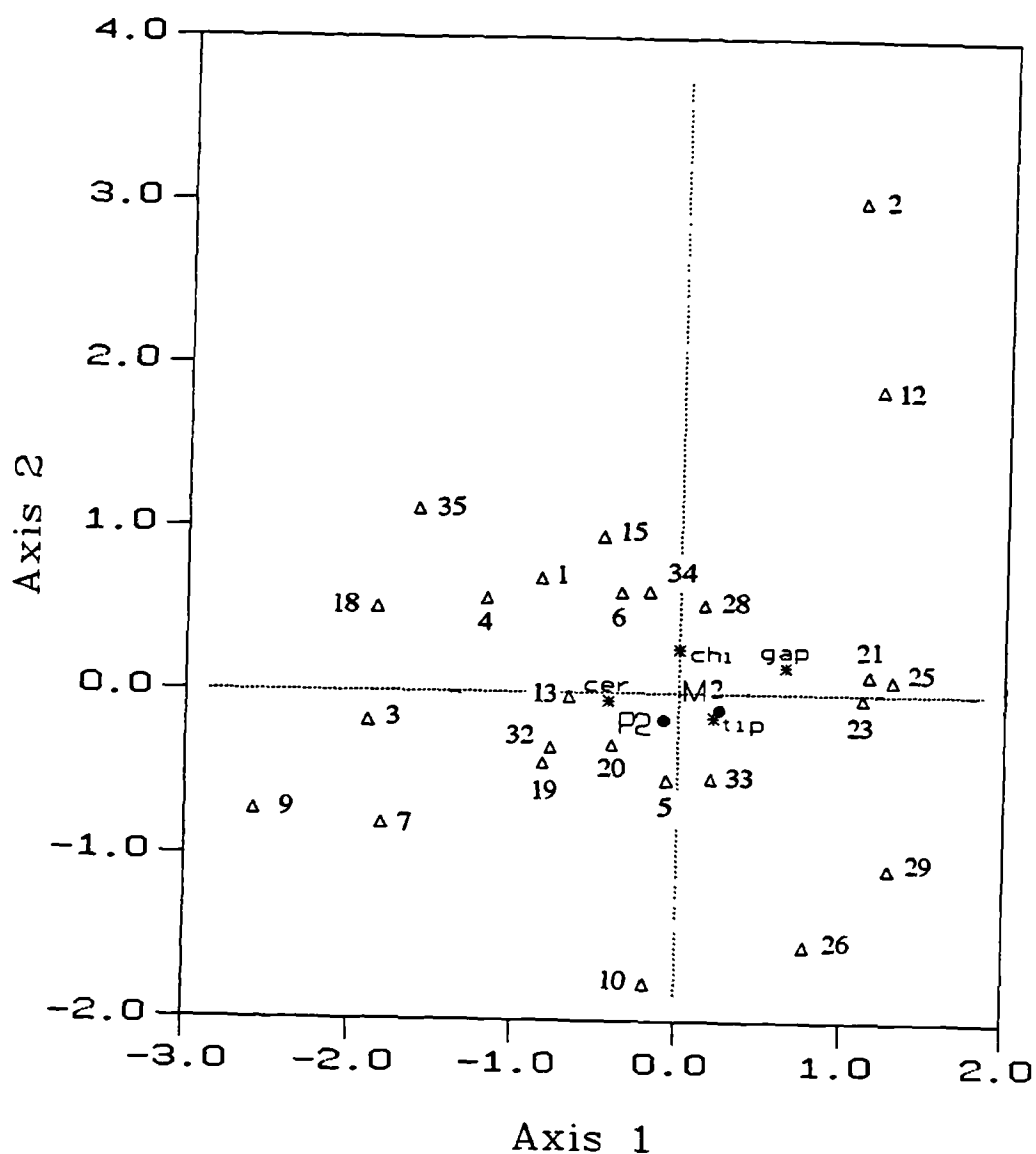
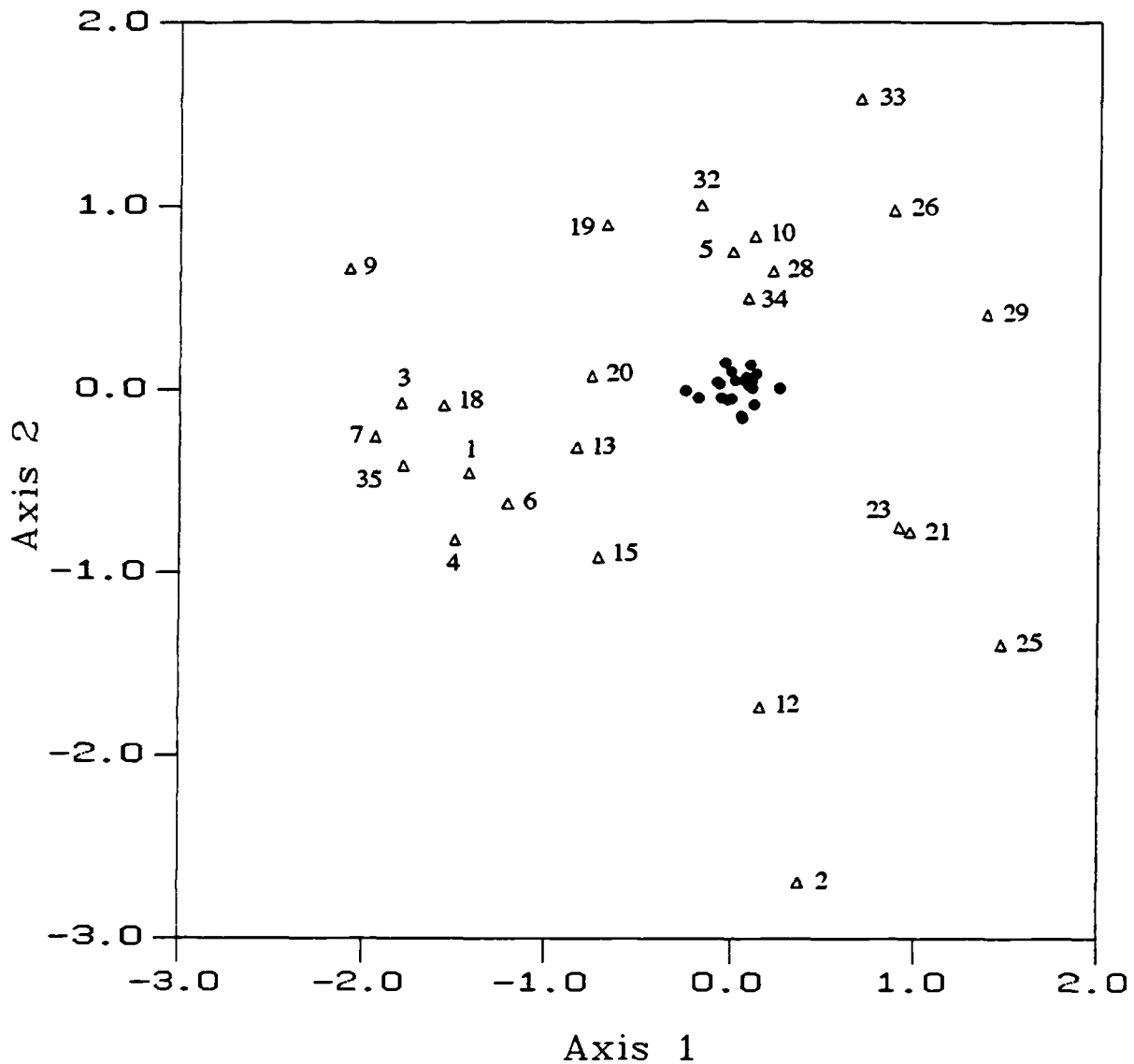


Fig. 6.7. Ordination biplot of the CCA results for all morphology traits without forward selection. Data were $\ln(x+1)$ transformed. Sites are shown as triangles and traits as black filled circles. The ordination was not statistically significant (Monte Carlo, $p>0.05$). For site names see Fig. 6.1.



was explained by the pairs of traits respectively. None of the traits were strongly correlated with Axis 1 or 2, and all traits were close to the origin ('short vectors').

The sites in the reproductive CCA biplot (Fig. 6.5) still seem to be separated out according to pH along Axis 1 with the acid sites to the left and the circumneutral sites to the right. This pattern is also found in the morphology biplot, although not as clearly. In general both biplots look very much like the initial DCA (Fig. 6.1), suggesting that latent variables were much more important in explaining species variance than the selected traits.

6.4 Discussion

There is thus no strong evidence from these data to support the theory that species traits differ between streams with contrasting environmental variables, at least not at the scale investigated. Although initially surprising, this finding has been supported by other research. Statzner *et al*'s (1997) very detailed study of reproductive traits involved an extensive world-wide literature search and included a large number of species. They found that larger females tended to lay larger unattached eggs in habitats that are 'stable' at the small scale (e.g. within wood or macrophytes), but unstable at the large scale (e.g. in temporary waters). Thus, only at a small scale did their observations correspond to the predictions of the habitat templet concept. Many other species had traits that did not show trends as predicted. In a detailed study of the River Rhône (Statzner *et al*, 1994), Usseglio-Polatera (1994) found that for only few of the life history traits of aquatic insects (minimum age of reproduction, number of reproductive cycles per year) did the trends agree with the predictions of the habitat templet theory. Townsend *et al* (1997) did, however, show a significant relationship between resistance/ resilience traits and spatial and temporal variation in a large-scale study of thirty-four tributary sites in New Zealand. They found that taxa possessing traits such as small size, high mobility, habitat generalism, streamlining, clinging and several life stages outside the stream were found in higher proportion than in more disturbed communities, although all traits

were represented in species throughout the templet. The New Zealand study differed from the other two in that many fewer *taxa* were used (often only identified to genera), but the environmental variables were measured and described more thoroughly (though not as thoroughly as in my study).

Many workers have suggested that the trade-off between species traits make distinct patterns unclear (Hildrew, 1986; Stearns, 1992; Roff, 1992; Resh *et al*, 1994; Statzner *et al*, 1997). Thus, there are many 'solutions' to the same ecological 'problem'. If an insect has a good hold-fast mechanism, for example, it can 'afford' to be larger or less mobile.

Another possible explanation is the problem of scale. At a very large scale streams are dominated by insects which in general are small, have short life cycles, large number of offspring, etc. At a small scale, Statzner *et al* (1997) found traits predicted by the templet, but these results were contradicted at a larger scale. The present study has compared traits that are important at various spatial and temporal scales. Streamlining and clinging, for example, are 'small-scale' traits; they are the answer to short-term (pulse) disturbance, where the trait permits survival of the individual without major changes to the life history of the organism. The organism may remain immobile during the event and proceed to contribute to a rapid re-establishment of community structure afterwards. During longer or more severe (press) disturbances, a favourable body shape may not in itself promote survival, as organisms may not be able to resist the disturbance over a long period of time. Instead, longer term/ larger scale traits, such as having life stages outside the stream, many offspring or prolonged ovipositioning periods might enhance survival of the overall population even though there may be considerable individual mortality. These types of traits may involve changes in life history, and recovery may take longer because populations recruit (many offspring, long ovipositioning period), or it may be more rapid because a large proportion of organisms were not affected by the disturbance (life stages outside the stream).

Townsend & Hildrew (1994) suggested that a mixture of species and traits might be found at undisturbed sites, but mainly species with resistance/ resilience traits would be found at high disturbance sites, due to higher mortality rates of species without those traits. Death (1995) found disturbed sites had very similar community compositions, whereas undisturbed sites had greater variation in community compositions compared both to disturbed sites and also to other undisturbed sites. The great mixture of traits found in this study might suggest that the streams investigated were all relatively undisturbed, if analysed in the light of Death's results.

Traits data were not available for all species. As Statzner *et al* (1997) pointed out, most information is available for common, abundant species which are more likely to exhibit a higher proportion of resistance/ resilience traits. Rarer species, for which information was not available, are more likely to be specialists that do not exhibit resistance/ resilience traits. Thus, the literature potentially lends bias towards species with particular traits.

In conclusion, this study did not find strong evidence to support the hypothesis that traits are a function of the habitat, at least not at the scale investigated. It seems likely that the fluvial habitat of streams requires all species to have at least some resistance/ resilience traits, and that the many different 'solutions' that evolution offers mean that an overall pattern is unclear.

CHAPTER 7: Colonisation.

* albeit for two traits per analysis only

7.1 Introduction

Chapter 6 showed that there were some, albeit weak, differences amongst streams with regards to species traits*, and that among the significant traits was poor dispersal ability. High mobility, or good dispersal ability, may be a very important resilience trait because many reports show that recolonisation is often rapid following disturbance (Boulton *et al*, 1988; Lake & Schreiber, 1990; Niemi *et al*, 1990).

Recolonisation of denuded areas may occur in a number of ways (Mackay, 1992). Drift has been suggested to be one of the most important methods of recolonisation (Townsend & Hildrew, 1976; Bird & Hynes, 1981; Benson & Pearson, 1987, but see Doeg *et al*, 1989). Swimming may be important in families such as the Baetidae and the Leptophlebiidae and in *Gammarus* (Hynes, 1970; Söderström, 1987), where the organisms may be able to swim considerable distances upstream, or actively leave the drift by swimming downwards. Nearly all benthic macroinvertebrates can crawl, and some do so rapidly. Research has shown that in some cases 50% of the mayfly larvae colonising substratum trays arrived by crawling (Richards & Minshall, 1988; Giller & Cambell, 1989). Other larger scale/longer-term methods of recolonisation, such as aerial dispersion, will not be discussed here.

Although lotic invertebrates in general colonise denuded substrata quickly, it is clear that some species are faster colonisers than others (Hemphill & Cooper, 1983; Boulton *et al*, 1988; Downes & Lake, 1991); these are the ^{species} fugitive _↓. Simuliidae, Baetidae and Chironomidae (Khalaf & Tachet, 1977; Lake & Doeg, 1985; Boulton *et al*, 1988) are good examples of rapid macroinvertebrate colonists in streams. These organisms often colonise denuded substratum in great numbers initially, and are later displaced or outcompeted by a greater range of organisms. Using total abundance as a measure of recolonisation is therefore often misleading, as abundances frequently reach pre-disturbance levels and above much sooner than communities reach former species richness or diversity levels or recover functionally (Milner, 1994)

Colonisation measures should include some degree of species richness or assemblage structure to avoid this problem.

Patterns of mobility in streams depend on a number of factors; one is whether communities are frequently affected by disturbances. A disturbance may be defined as "any relatively discrete event in time that removes organisms and opens up space or other resources that can be utilised by individuals of the same or different species" (Hildrew & Townsend, 1987; Townsend, 1989). Thus, a disturbance involves the removal of organisms, and assumes low community resistance. During a disturbance a combination of refugium use and/or high mobility might lower mortality. Refugia may be localised undisturbed patches or, on a larger scale, upstream areas or tributaries. The effect of disturbances on stream communities may be lowered if organisms are able to move into refugia before being washed away. There is some evidence that meiofauna actively move further down into the hyporheic zone immediately before a disturbance, thus lowering mortality (Schmid-Araya, 1993; 1994). Even once organisms are entrained in the drift, the presence of flow refugia may limit the distance they are transported (Lancaster *et al*, 1996: Appendix 1), and some organisms of high mobility may actively leave the drift, thus further limiting the effect of the disturbance (Ciborowski & Corkum, 1980; Lancaster *et al*, 1996). Rapid recolonisation depends on the ability of organisms to disperse from unaffected areas following a disturbance. Thus, high mobility is potentially a very important resilience trait, and rapid recolonisation is expected to be apparent in streams that are frequently disturbed.

Although the previous Chapter indicated that mobility only differed weakly between streams, those analyses were based on a limited number of species, and on information retrieved from the literature. There was, therefore, no account taken of the possible influence of species composition or habitat type. Mobility may not solely be linked to disturbance and it is, for example, possible that the presence of certain predators or of food (Kohler, 1984; 1985) or a more frequent disturbance regime might cause increased mobility of some species compared to situations or habitats

without those factors. A species reported to be very mobile in a disturbed stream with a high density of predators may, thus, be naturally less mobile in an undisturbed stream with few predators. Any real differences between the streams examined could be discovered only by experimental manipulation.

The experiment described in this Chapter, therefore, attempted to examine differences in the dispersal ability of benthic macroinvertebrates inhabiting streams with differing environmental variables, and in particular with different disturbance frequencies and refugium availabilities. The specific hypothesis was that the colonisation rate (resilience) in very disturbed streams should be higher than in less disturbed streams. Colonisation is expected to increase with discharge in all streams, but at a greater rate in more frequently disturbed streams, where higher dispersability could be an adaptation to disturbance. Colonisation of cleaned natural substrata was used as an indicator of dispersal/mobility.

7.2 Methods

7.2.i Experimental design

Cages were used to measure colonisation rates of macroinvertebrates in seven streams which differed in disturbance frequency and refugium availability (Table 7.1). Cages were of the dimensions 12.7 cm width x 17.75 cm length x 5.75 cm depth

Table 7.1. Sites used for the colonisation experiment. Sites are listed in order of decreasing disturbance frequency.

Stream	Disturbance frequency	Stream 'Type'	pH range
Boringwheel Mill (BWM)	1.0000	II	5.3-7.1
Batt's Bridge (BB)	0.0821	III	5.3-7.4
Marsh Green (MG)	0.0493	III	4.4-6.8
Broadstone Stream (BS)	0.0438	I	4.0-6.2
Old Forge (OF)	0.0383	II	5.5-7.0
Withyham (WY)	0.0273	III	5.4-6.7
Below Friar's Gate (BFG)	0.0273	II	5.0-6.3

Plate 7.1. Colonisation cage



photograph courtesy of Stuart Orton

(Plate 7.1); the base was made of rigid plastic (a lunch box lid) and the four sides and the top of the cages were made of garden mesh (15mm) which allowed free access to invertebrates. The cages were filled with cleaned substratum taken from the stream bed of each individual site. This substratum was chosen over a uniform one, as research has shown that invertebrates may preferentially colonise substratum of intermediate particle sizes (Brooks & Boulton, 1991). Since there was a distinct difference in particle sizes between streams, the use of 'native' substratum minimises this effect. The substratum was cleaned by washing and rubbing each individual stone (in the case of the six sites with coarse substratum); at Batt's Bridge, where the substratum is considerably finer, the stones were placed in a bucket which was vigorously swirled around and emptied. This was repeated several times to ensure all animals had been removed. As no attempts were made to remove anything but the animals, the substratum in the cages was presumed to be identical to that outside the cages, although the biofilm may have been affected.

At each site ten cages were placed in riffles, partially embedded in the stream bed so that the stones in the cages were level with the stones outside. Cages were placed longitudinally so that the shortest sides were facing up- and downstream. The positioning of cages in rows was staggered, making sure that upstream cages were not immediately sheltering cages downstream of them.

Half the cages were removed after two days, the other half after seven days. A pond net (mesh 330 μ m) was placed immediate downstream from the cage, which was quickly scooped into the net. Stones were washed inside the net and placed back in the cages, and the contents of the pond net was placed in a plastic bag and preserved in 70% methylated spirits. At Batt's Bridge the contents of the cage were scooped into a bucket, which was swirled vigorously for approximately ten seconds, after which the water holding the animals was quickly but carefully tipped into the net. This process was repeated three times. The cages were either left at the side of the stream (day 2) or placed back in the stream (day 7) for the next run.

Discharge was measured on each occasion. The details of these measurements are given in Chapter 3. As discharge is likely to affect colonisation rates, and any differences between streams might be most apparent at high discharges, a range of discharges was needed for the experiment. The experiment was carried out almost every week over a period of five months (between 16-10-95 and 28-2-96). In the end, due to lack of precipitation, only two occasions of high discharge were recorded, and data were used for these and from three occasions of low and three of medium discharge.

Every two weeks five Surber samples were taken in riffles to determine background community composition. These samples were taken away from the site where the cages were so as to not affect them and, once sampled, the area was left for at least two months before sampling again. Sampling every two weeks ensured that the streams would either have been sampled on the day corresponding to day 0 or day 7 of the cages.

The samples were taken back to the laboratory where they were sorted and invertebrates were identified to species level where possible. The Chironomidae were identified only to subfamily.

7.2.ii Data analysis

Multivariate statistics were used on the data sets. The use of multivariate statistics is described in detail in Chapter 5. A DCA was first performed on the complete species & site data set to see whether a linear or unimodal model should be used. The species abundances were transformed to percentages to avoid the problem of differences in abundances between sites. It has already been determined that the low pH sites are more species poor and have lower abundances than the more circumneutral sites (Chapter 5), and this is not the pattern being tested here.

A CCA was then performed to see how well the environmental variables explain the variance in species data. A clear arch was shown on the biplot, so the analysis was repeated using DCCA instead. To test whether disturbance frequency

and refugium availability significantly explained species variance on their own and to see how the sites were placed in a biplot in relation to these variables, a CCA was run with all but disturbance frequency and stream 'Types' as covariables. Monte Carlo tests were performed to test the validity of the analyses.

In order to discover patterns in this very large data set, it was split up into a number of smaller data sets:

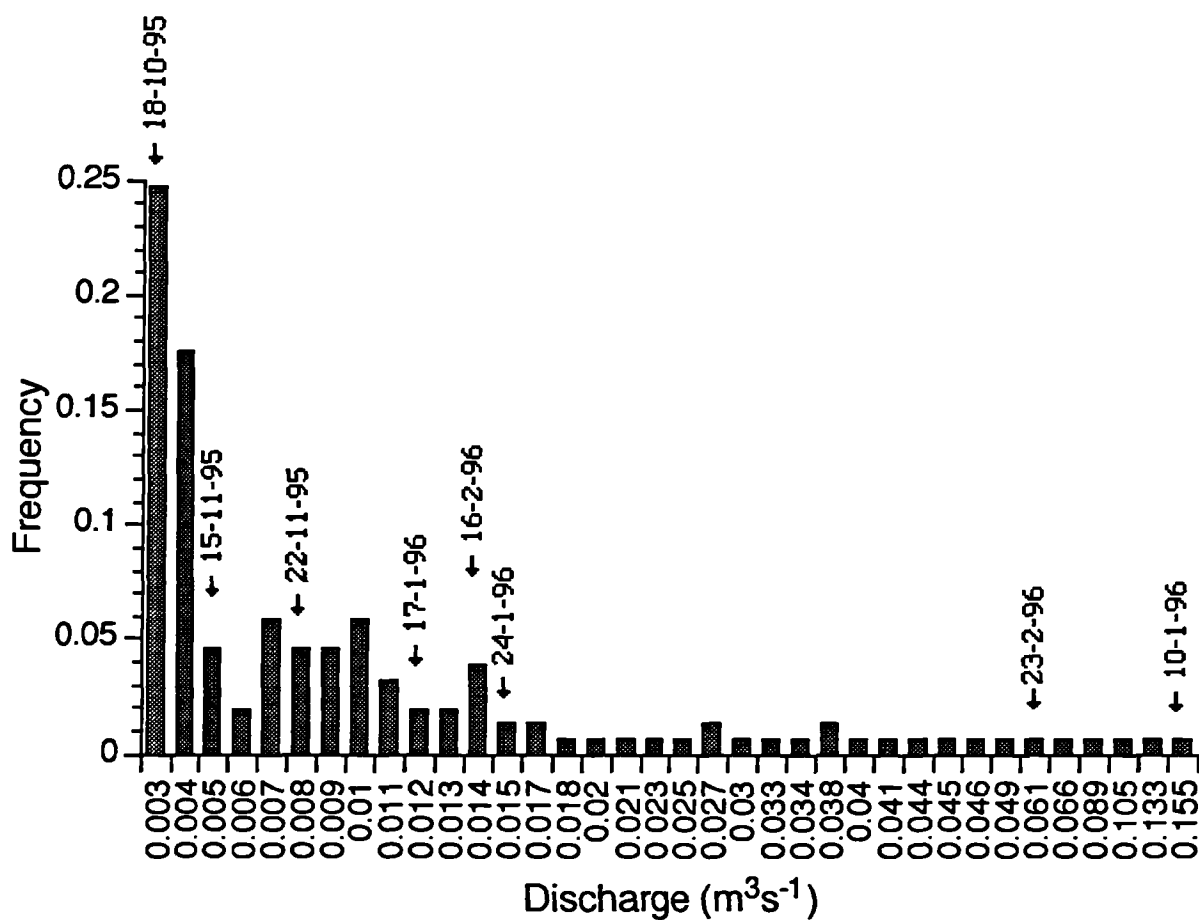
- The Day 2, Day 7 and background Surbers were tested on their own at every date, for every site. This was done to see how much each type of sample varied over time and with different discharge.
- Each site was tested on its own on all dates to highlight within-site variations, i.e. in order to determine whether colonisation rates at that site varied significantly with discharge.
- All the sites were then tested on one single date to highlight between-site variations, i.e. to see whether discharge affected the sites differently.

Colonisation rates are obviously affected by the supply of potential colonists, and these are estimated by the background Surbers. Relative colonisation rates, or the "Mobility Index" (Winterbottom *et al.*, 1997b) were calculated for the total number of species in each stream on each occasion:

$$(\text{total no. of organisms per m}^2 \text{ of Cage} / \text{total no. of organisms per m}^2 \text{ of Surber})$$

The relationship between mobility index and discharge was examined using regression analysis, and an analysis of covariance (ANCOVA) was used to check for homogeneity of slopes and elevations. The mobility index ($\ln(x+1)$ transformed) was used as the dependent variable in the ANOVA, with peak intervening daily discharge ($\log(x+1)$ transformed) as the covariate. A *post hoc* test (Tukey) was then used to compare pairs of regression lines. These analyses were carried out using SYSTAT for the Apple Macintosh (Wilkinson, 1992). Abundances often reach background levels and above very rapidly (Milner, 1994), due to a few opportunistic species colonising in great numbers. Calculating colonisation rates from abundance data therefore

Fig. 7.1. Frequency distribution of discharges for Broadstone Stream, October 1995 - February 1996. Arrows show discharge on sampling-dates which were included in the final analyses.



seldomly reflects a return of the community to pre-disturbance levels, but may be a reflection of the proportion of opportunistic, or high mobility, species in the communities.

7.3 Results

Eight dates were chosen for which the samples were sorted and identified; three each of low and medium flow and, due to the exceptionally dry autumn and winter of 1995-96, only two of high flow (Table 7.2 & Fig. 7.1).

Table 7.2. Dates chosen and their maximum discharges within the week.

Year	Date (day 2 of each week)	Discharge at Broadstone (m^3s^{-1})	Flow
1995	October 18th	0.0031	'low'
	November 15th	0.0052	'low'
	November 22nd	0.0080	'low'
1996	January 10th	0.1553	'high'
	January 17th	0.0125	'medium'
	January 24th	0.0152	'medium'
	February 16th	0.0147	'medium'
	February 23rd	0.0607	'high'

Each date signifies a week, and within that week there are three data points (day 2, day 7 and background Surber). The closer the points are to each other on the ordination biplot, the more alike they are; thus, if the cage and Surber points are very close together, this could mean either that the colonisation rates are rapid, or that the background densities have decreased and are more like the low-abundance cages.

7.3.i Effect of environmental variables on the complete unsplit data set

The DCA of the percentage species abundance data for the complete data set (all sites, all dates) calculated a gradient length of 3.494 (Table 7.3), thus unimodal models were used for further analyses. The Eigenvalues were quite high (0.561 and

Table 7.3. DCA of total data set. Data were percentage transformed and rare species downweighted.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.561	0.320	0.237	0.149
Gradient lengths	3.494	2.863	2.710	2.369
cumulative % variation of species data	14.5	22.9	29.0	32.9
Sum of all unconstrained Eigenvalues				3.854

0.320 for Axis 1 and 2 respectively), indicating good separation along the axes, although only 22.9% of the species variation was explained by the first two axes.

A CCA was performed to discover what effect the environmental variables had on the species data. The biplot of the CCA turned out to have an arch effect, so the analyses were repeated using DCCA instead (Table 7.4 & Fig. 7.2). The

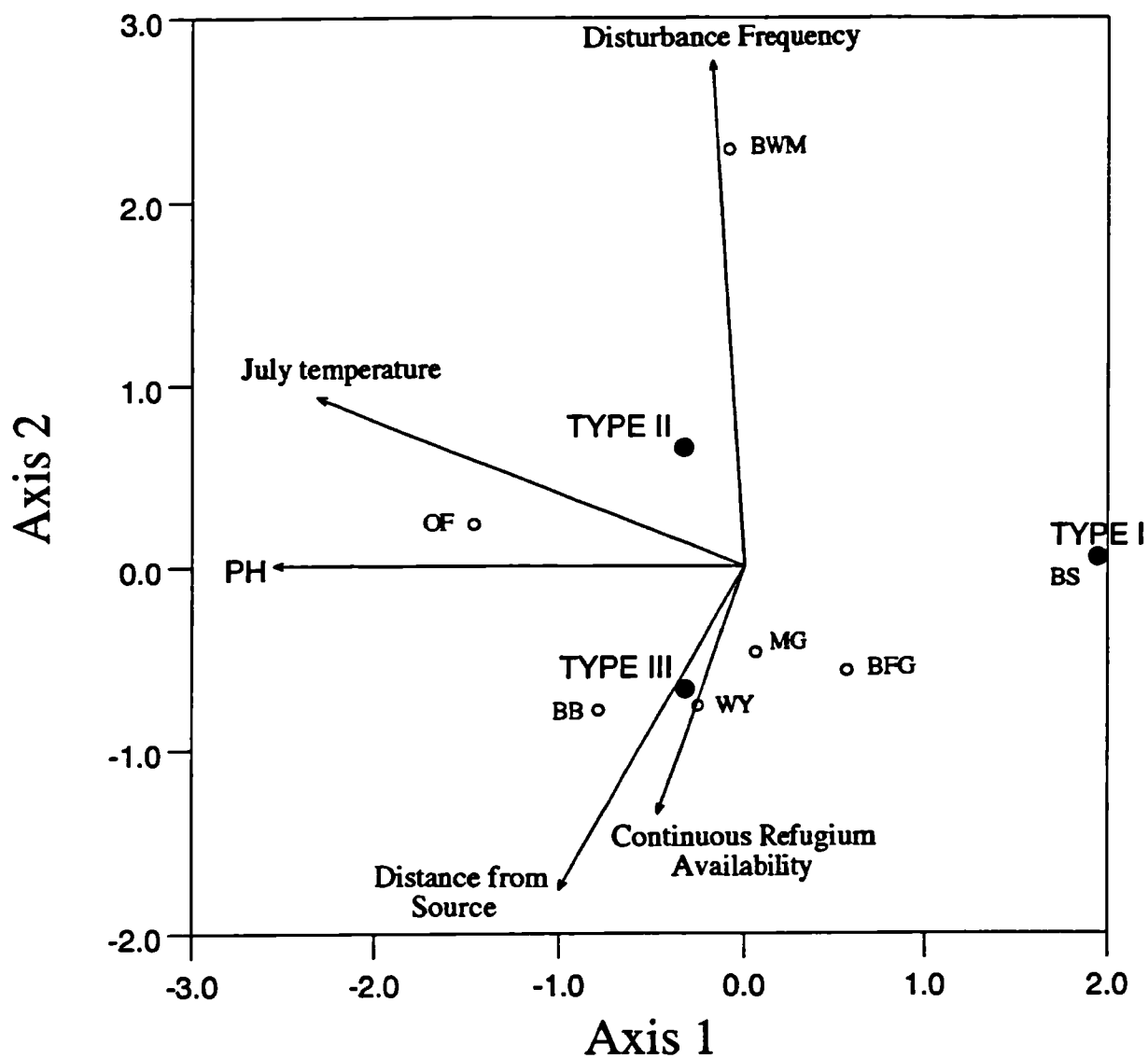
Table 7.4. DCCA of total data set. Data were percentage transformed and rare species downweighted.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.510	0.321	0.101	0.359
Cumulative % variation of species data	13.2	21.6	24.2	33.5
Sum of all unconstrained Eigenvalues				3.854
Sum of all canonical Eigenvalues				1.486
Monte Carlo	Axis 1: Overall:			
(99 permutations under full model)	p=0.01	p=0.01		

Eigenvalues were high (0.510 and 0.321 for Axis 1 and 2, respectively), while 21.6% of the variation was explained by the first two axes, and 38.6% (1.486/3.854) of the total variance was explained by the environmental variables measured. Axis 1 was most strongly correlated with high refugium availability (Type I), and negatively correlated with pH. Axis 2 was strongly correlated with disturbance frequency. Each of the seven sites were placed on the biplot in relation to these variables. As the environmental variables for each site do not vary between sampling occasions (pH was only measured once, July temperature, disturbance frequency, and refugium availability are constants), all sampling occasions for each site have identical environmental variables and, therefore, each site is represented in only one point on

Fig. 7.2. DCCA of the total data set (seven streams, eight sampling occasions, Surbers and cages). Data were percentage transformed and rare species were downweighted. Sites are shown as open circles, stream 'Types' are dark circles, and continuous environmental variables are vectors.

Site coding is given in Table 7.1 (page 139).



the biplot. As Broadstone was the only Type I stream, the Type I dark circle and the open circle for Broadstone are in the same spot (Type I is highly associated with Broadstone).

A CCA was then performed with pH, distance from source, continuous refugium availability and July temperature as covariables (Table 7.5 & Fig. 7.3).

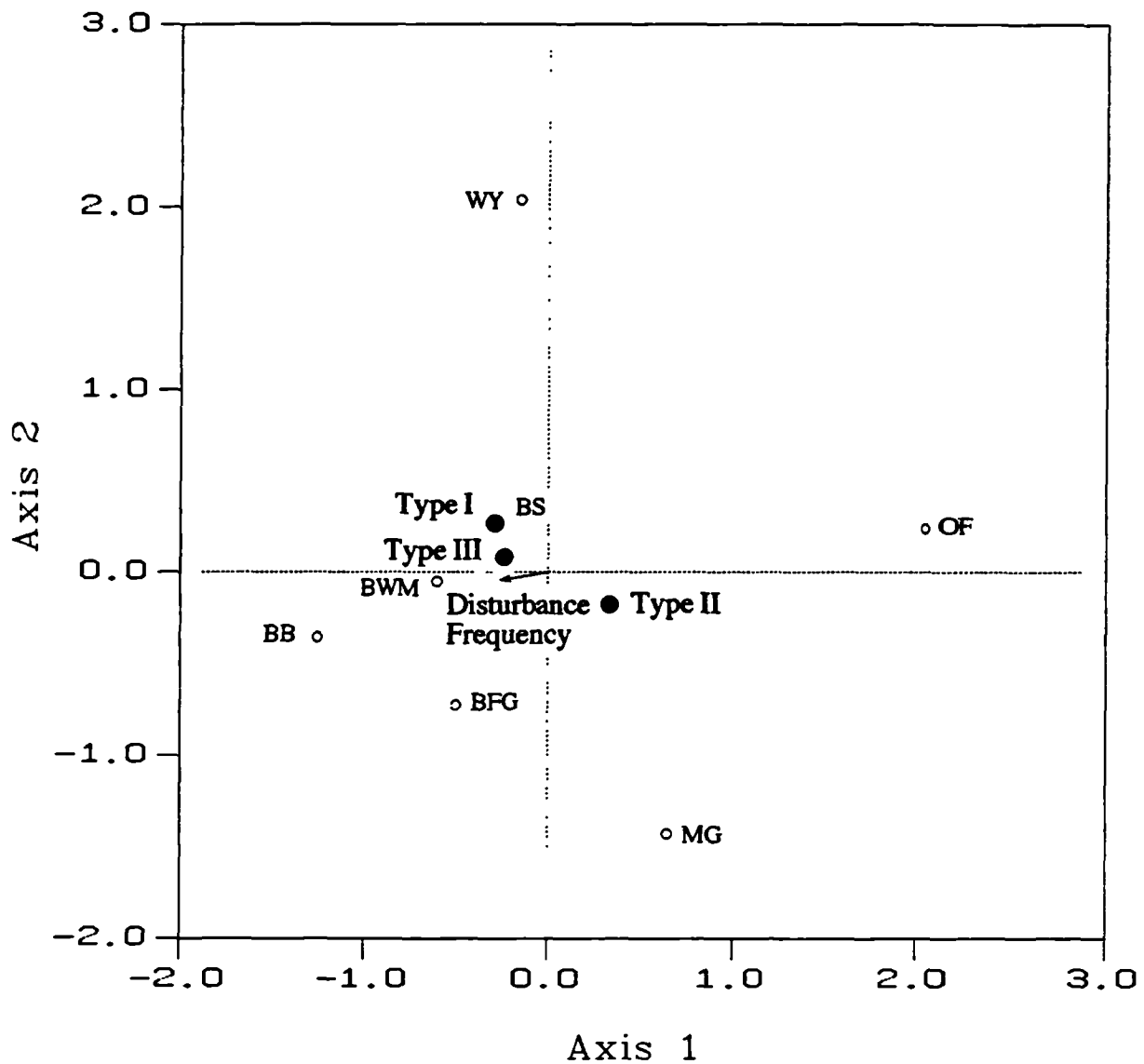
Table 7.5. CCA with pH, distance from source, continuous refugium availability and July temperature as covariables. Data were percentage transformed and rare species were downweighted.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.236	0.105	0.359	0.183
Cumulative % variation of species data	8.7	12.6	25.8	32.6
Sum of all unconstrained Eigenvalues				2.709
Sum of all canonical Eigenvalues				0.341
Monte Carlo	Axis 1: Overall:			
(99 permutations under full model)	p=0.01	p=0.01		

Thus, only disturbance frequency and stream 'Type' were left to be entered as environmental variables. Eigenvalues were reduced (0.236 and 0.105 for Axis 1 and 2, respectively) and the environmental variables now explained only 12.6% (0.341/2.709) of the total variance. The Eigenvalues for Axis 3 were higher than those for Axis 2; this suggests that only Axes 1 and 2 were constrained. Axes are constrained by environmental variables imposed on the analysis. Unconstrained axes are those where the analysis maximises dispersion without the constraint of an imposed variable. It is said that 'latent' (or hypothetical variables) maximise the dispersion along those axes. In this case, although four environmental variables were entered (Disturbance frequency & Types I, II and III), the Eigenvalues indicate that only two of the four variables were significant. Axes 3 and 4 were therefore 'unconstrained'. The placement of the seven streams in relation to these two environmental variables can therefore be thought of as the habitat templet. The fit was significant (Monte Carlo, $p=0.01$).

Another CCA was run omitting Boringwheel Mill, as the disturbance frequency for this site was much higher than for the other sites, and this site has been

Fig. 7.3. CCA of the total data set (seven streams, eight sampling occasions, Surbers and cages). Distance from source, pH, continuous refugium availability and July temperature were entered as Covariables. Data were percentage transformed and rare species were downweighted. Sites are shown as open circles, Stream 'Types' are dark circles, and Disturbance Frequency is shown as a vector.



shown to affect the analysis (Chapter 6). Only one axis was now constrained, as the significance of disturbance frequency was reduced, and the percent species variance explained was lower (5%).

7.3.ii. Background Surbers, Day 2 & 7 Cages, all sites, all dates

Background Surbers and Day 2 and 7 Cages were analysed independently of each other for each site on all dates to give an idea of how much natural variation there was in the background communities and in the cages. Thus, this analysis investigates natural variations in communities and the effect discharge has on them.

An initial DCA was performed for each of the three data sets: Surbers, Day 2 Cages and Day 7 Cages. All gradient lengths in this data set were greater than 2.0, so the DCAs were used for further analyses. The Eigenvalues were high (between 0.547 and 0.607) (Table 7.6), and between 25 and 26.9% of the variance in the species data was explained by the first two axes.

Table 7.6. DCA percentage transformed data, background Surbers, Day 2 & 7 cages, all sites, all dates.

	Axis 1	Axis 2	Axis 3	Axis 4
Background Surbers:				
Eigenvalues	0.607	0.387	0.187	0.106
Gradient lengths	3.727	2.806	2.446	1.771
Cumulative % variation of species data	16.4	26.9	32.0	34.8
Sum of all unconstrained Eigenvalues				3.692
Day 2 cages:				
Eigenvalues	0.572	0.395	0.266	0.117
Gradient lengths	3.478	2.976	2.740	2.244
Cumulative % variation of species data	14.8	25.0	31.9	34.9
Sum of all unconstrained Eigenvalues				3.863
Day 7 cages:				
Eigenvalues	0.547	0.328	0.191	0.104
Gradient lengths	3.209	2.689	2.002	2.214
Cumulative % variation of species data	16.6	26.5	32.3	35.4
Sum of all unconstrained Eigenvalues				3.299

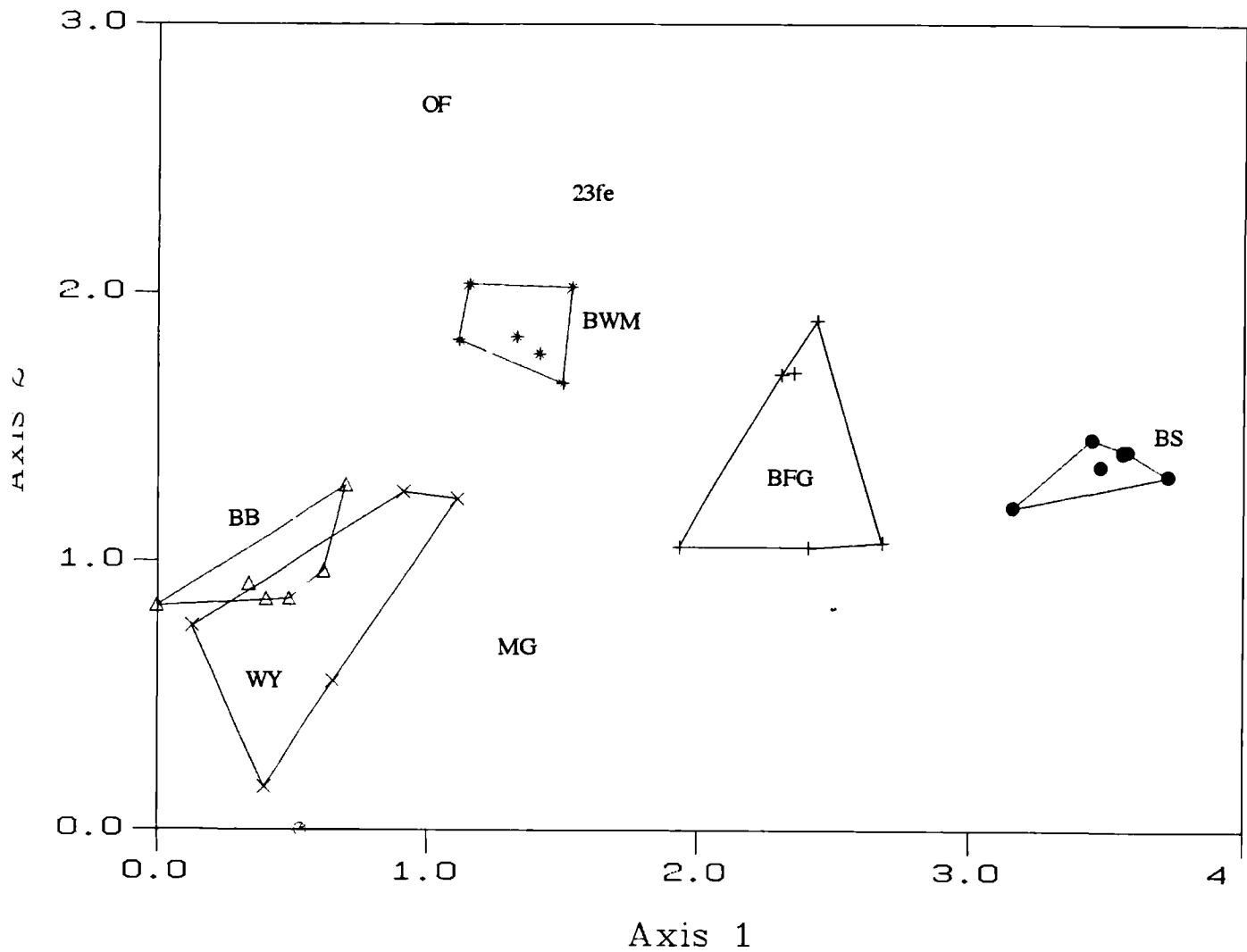
The biplot (Fig. 7.4a) for the background Surber data showed how each individual site varies naturally in a year. Each cluster represents a site, and each point on the graph represents the sum of the five Surbers taken on each date. For instance, the light blue cluster at the top left hand corner of the biplot are all Surbers taken for Old Forge. The points (dates) are highly clustered, except for 23rd February which lies slightly away from the others. This indicates that the background communities (Surbers) were very similar on all dates, with the possible exception of on the 23rd February (one of the high flow occasions). Thus, Old Forge, Boringwheel Mill, Broadstone Stream and Batt's Bridge show very little variation throughout the year, Below Friar's Gate shows moderate variation, and Marsh Green and Withyham generally show high variation.

The Day 2 Cage communities were much more varied than the background communities (Fig. 7.4b). This pattern is not surprising, as colonising communities are expected to vary stochastically depending on initial arrivals. The biplot reflects this variation, where in some cases colonists in one stream were more similar to colonists in other streams than they were to other Cage 2 colonists on different dates in the same stream. This pattern is shown by the overlap of the clusters on the biplot; one of the colonising communities (23rd February) in Batt's Bridge (top left on the biplot) was more similar to the majority of the colonising communities in Withyham than it is to other Batt's Bridge cage assemblages. Communities at most sites varied greatly, with the exception of Below Friar's Gate, where colonising communities were very similar at all discharges. The pattern seen for the day 7 cage communities was very similar to that for Day 2, except variations in some cases were slightly smaller (Fig. 7.4c). There was less overlap between sites, and communities had become more distinct.

Fig. 7.4. DCA ordination biplots of a) Background Surbers; b) Day 2 Cages; c) Day 7 Cages. All sites on all sampling occasions. Data were percentage transformed.

Year	Date	Discharge at Broadstone (m ³ s ⁻¹)	Flow
1995	October 18th	0.0031	'low'
	November 15th	0.0052	'low'
	November 22nd	0.0080	'low'
1996	January 10th	0.1553	'high'
	January 17th	0.0125	'medium'
	January 24th	0.0152	'medium'
	February 16th	0.0147	'medium'
	February 23rd	0.0607	'high'

Fig. 7.4a Background Surbers



Where:

- BB = Batt's Bridge
- BFG = Below Friar's Gate
- BS = Broadstone Stream
- BWM = Boringwheel Mill
- MG = Marsh Green
- OF = Old Forge
- WY = Withyham

Fig. 7.4b Day 2 Cages

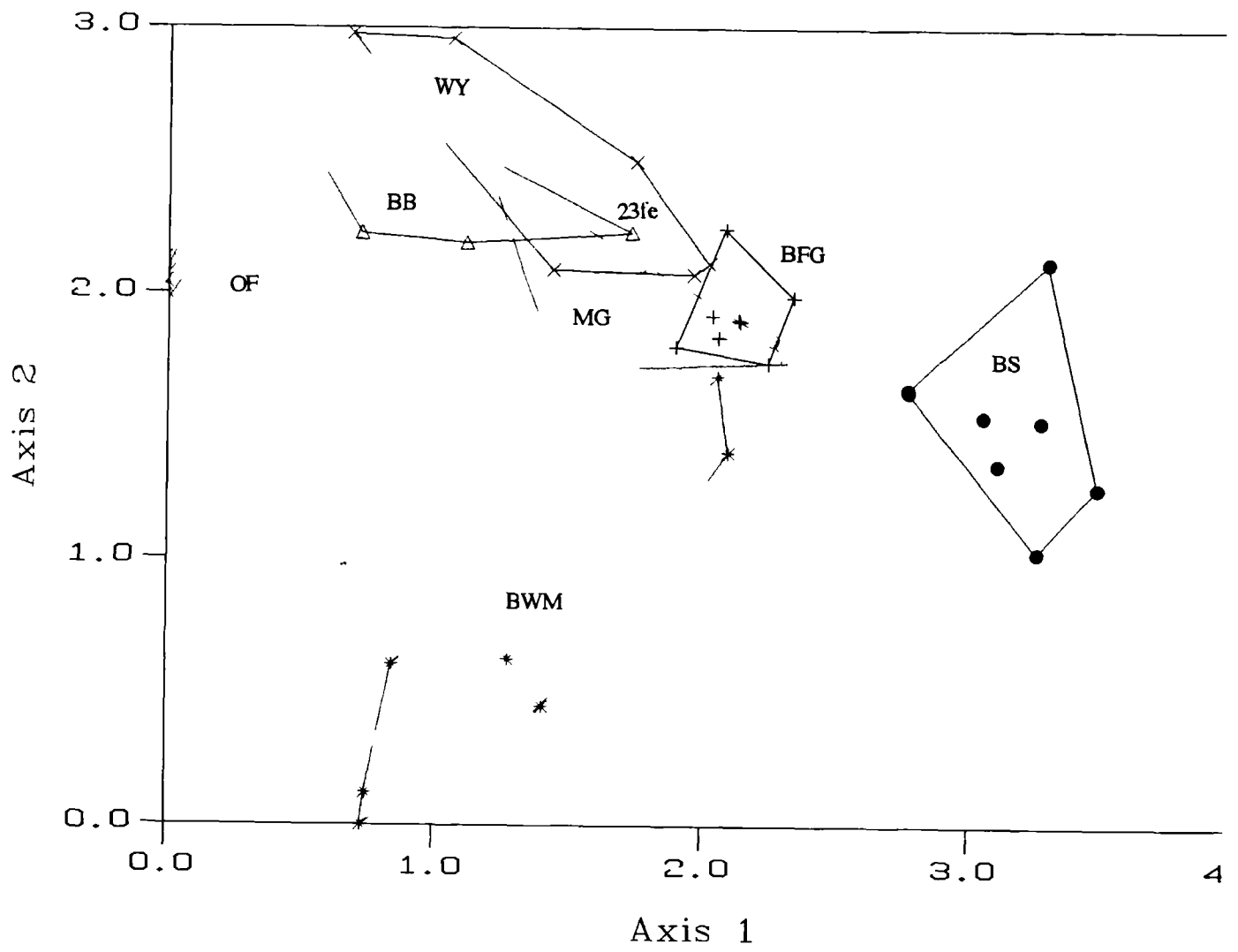


Fig. 7.4c Day 7 Cages

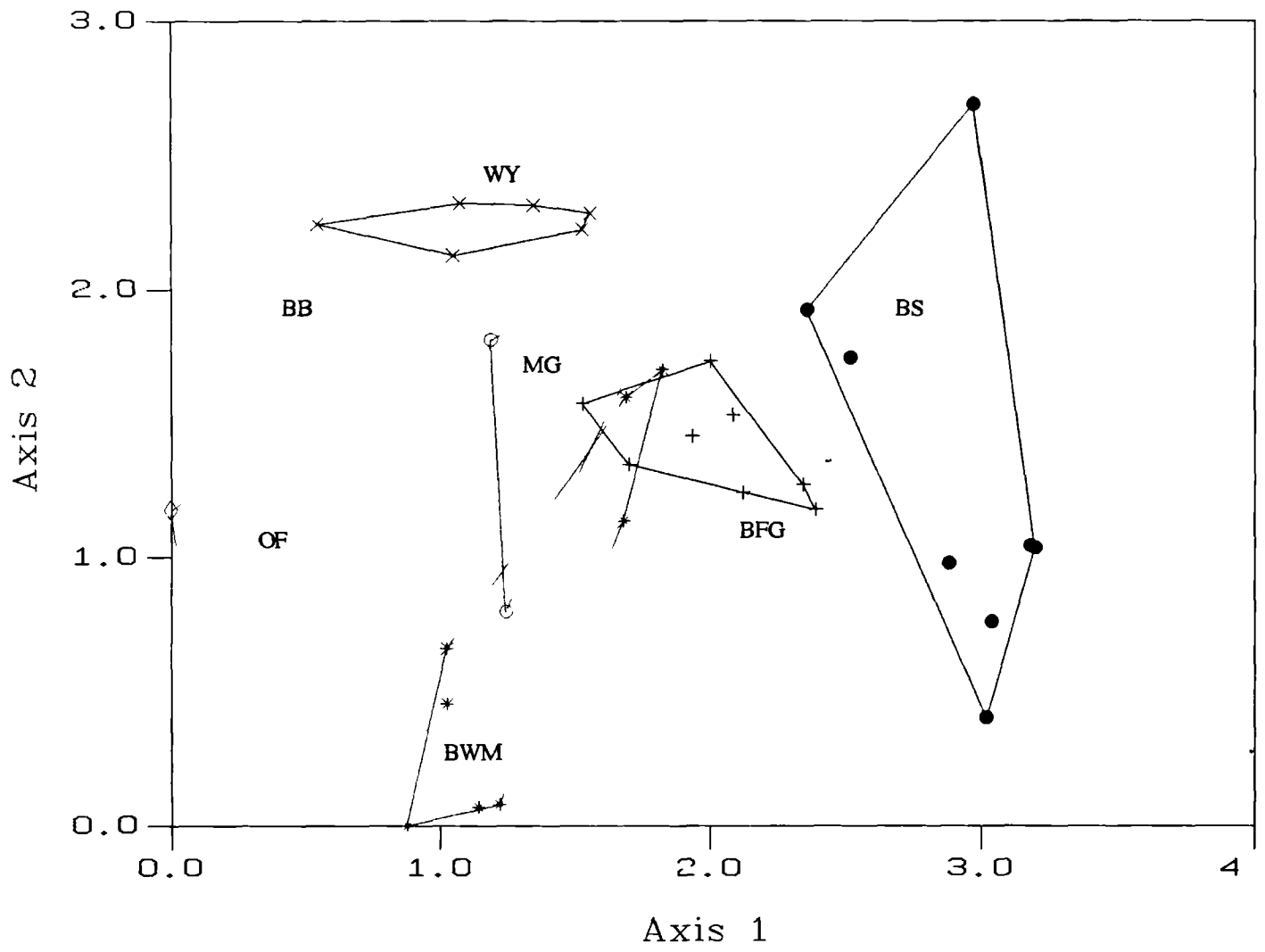


Table 7.7. DCA of raw data (not percentage transformed). Single site, all dates.

	Axis 1	Axis 2	Axis 3	Axis 4
Broadstone Stream:				
Eigenvalues	0.363	0.246	0.089	0.040
Gradient lengths	2.104	1.962	1.452	1.108
Cumulative % variation of species data	24.5	41.1	47.1	49.8
Sum of all unconstrained Eigenvalues				1.482
Boringwheel Mill:				
Eigenvalues	0.393	0.201	0.030	0.012
Gradient lengths	2.399	1.860	1.327	1.177
Cumulative % variation of species data	30.3	45.8	48.1	49.0
Sum of all unconstrained Eigenvalues				1.297
Below Friar's Gate:				
Eigenvalues	0.202	0.085	0.039	0.017
Gradient lengths	1.479	1.439	1.327	0.854
Cumulative % variation of species data	22.9	32.5	36.9	38.8
Sum of all unconstrained Eigenvalues				0.884
Marsh Green:				
Eigenvalues	0.575	0.179	0.037	0.02
Gradient lengths	2.873	1.984	1.689	1.411
Cumulative % variation of species data	35.0	45.9	48.2	49.4
Sum of all unconstrained Eigenvalues				1.642
Old Forge:				
Eigenvalues	0.325	0.094	0.021	0.014
Gradient lengths	1.825	1.128	1.165	0.780
Cumulative % variation of species data	31.2	40.2	42.2	43.5
Sum of all unconstrained Eigenvalues				1.044
Withyham:				
Eigenvalues	0.553	0.087	0.057	0.024
Gradient lengths	2.850	1.558	1.327	1.021
Cumulative % variation of species data	35.8	41.4	45.1	46.6
Sum of all unconstrained Eigenvalues				1.547
Batt's Bridge:				
Eigenvalues	0.363	0.156	0.043	0.026
Gradient lengths	2.224	1.533	1.225	1.046
Cumulative % variation of species data	28.6	40.8	44.2	46.3
Sum of all unconstrained Eigenvalues				1.271

7.3.iii Single site all dates

Each site was analysed independently on all dates to indicate how discharge affects colonisation rates at each site. Thus, this type of analysis investigates the effects of discharge within sites.

All but two DCAs calculated gradient lengths over 2 (Table 7.7), and the DCA results were used in the ordination biplots for those sites. Old Forge and Below Friar's Gate had gradient lengths less than 2, so PCAs (linear response models) were run on the data for those sites instead (Table 7.8), and the results from these were used in the biplots. Eigenvalues of the DCAs were high (all over 0.30), and over 40% of species variance was explained by the first two axes in all cases. The total sum of squares (TSS) of the species data in PCAs are always equal to 1. Eigenvalues are fractions of the TSS, and the sum of all Eigenvalues in a PCA is equal to 1. The Eigenvalues in the two PCAs are high, indicating that between 47.9% and 53.3% of the species variance is explained by the first two axes.

Table 7.8. PCA of Below Friar's Gate and Old Forge, the two sites with a DCA gradient length less than 2. Data were $\ln(x+1)$ transformed and centred.

	Axis 1	Axis 2	Axis 3	Axis 4
Below Friar's Gate:				
Eigenvalues	0.416	0.117	0.102	0.065
Cumulative % variation of species data	41.6	53.3	63.4	69.9
Total sum of squares				1.00
Old Forge:				
Eigenvalues	0.354	0.125	0.100	0.079
Cumulative % variation of species data	35.4	47.9	58.0	65.8
Total sum of squares				1.00

The different colonisation patterns between streams are best seen in the ordination biplots (Figs. 7.5a-g). In these biplots each individual biplot represents one stream. The similar symbols, which in some streams have hulls drawn around them, represent Surbers, Day 2 and Day 7 cages from one week and, therefore, one discharge. Thus, for example, the cluster of green open circles in the top left corner of the Broadstone

Fig. 7.5. DCA ordination biplots of a) Broadstone Stream; b) Batt's Bridge; c) Boringwheel Mill; d) Marsh Green; e) Withyham. PCA ordination biplots of f) Old Forge; g) Below Friar's Gate. Single sites, all dates. Raw data were used (no transformations).

Year	Date	Discharge at Broadstone (m ³ s ⁻¹)	Flow
1995	October 18th	0.0031	'low'
	November 15th	0.0052	'low'
	November 22nd	0.0080	'low'
1996	January 10th	0.1553	'high'
	January 17th	0.0125	'medium'
	January 24th	0.0152	'medium'
	February 16th	0.0147	'medium'
	February 23rd	0.0607	'high'

Fig. 7.5a Broadstone Stream

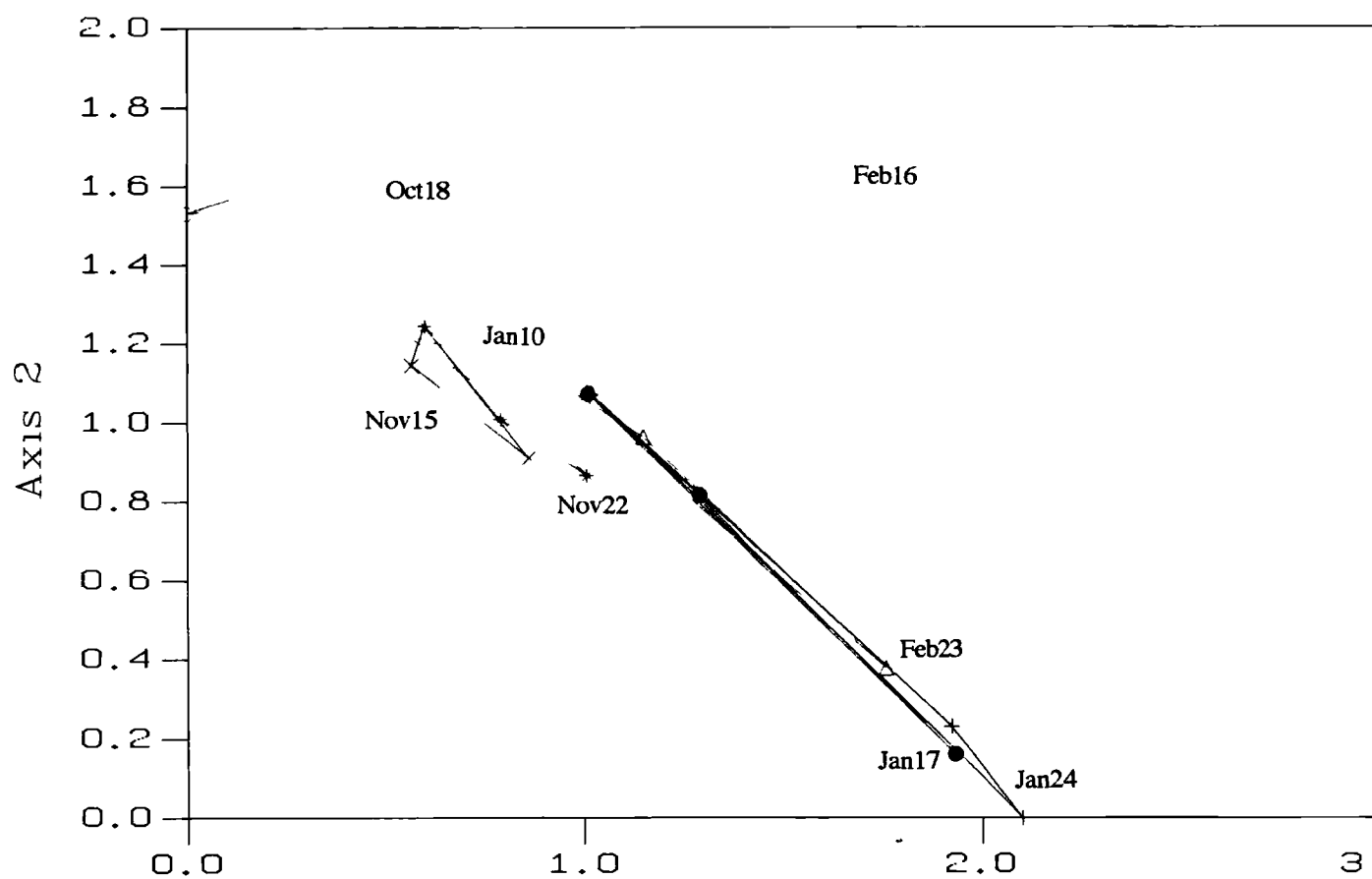
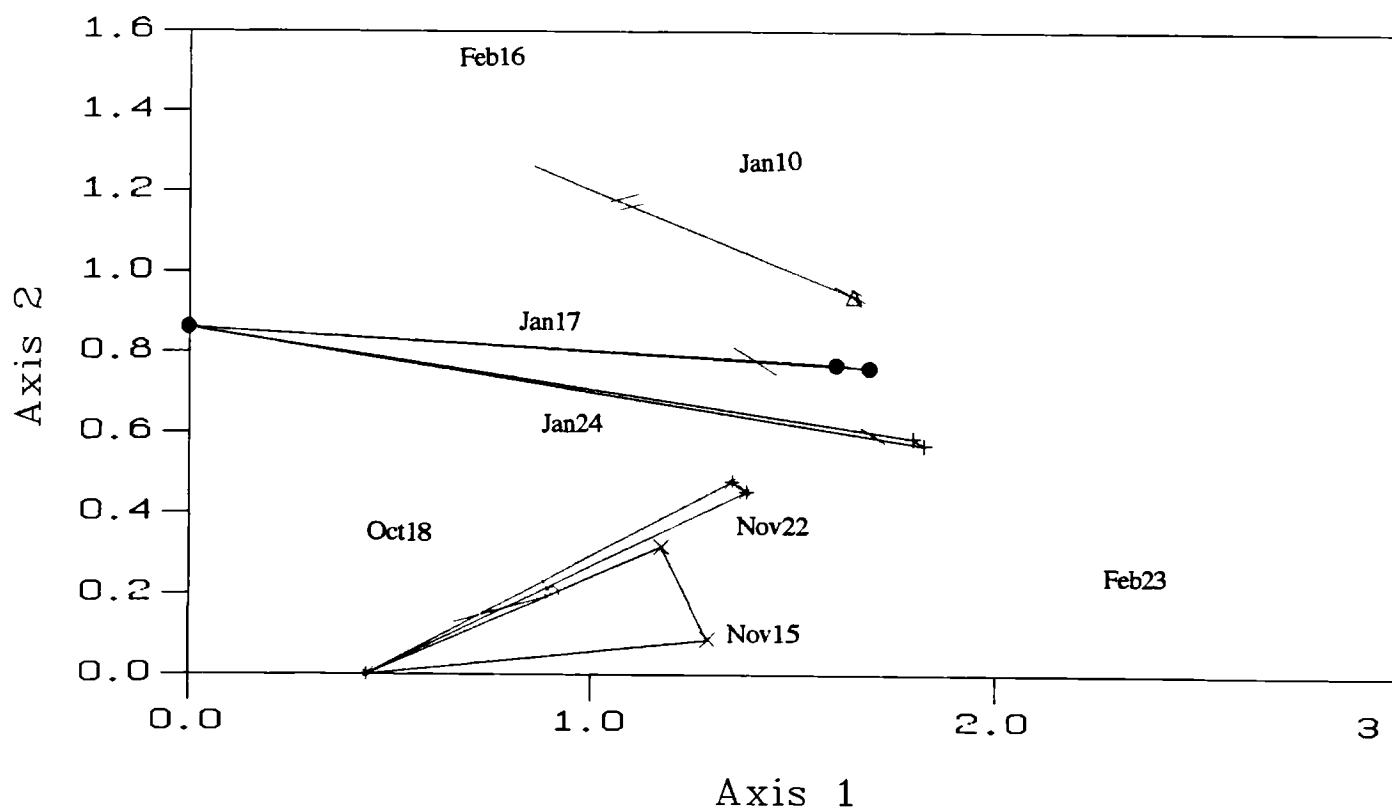


Fig. 7.5b Batt's Bridge



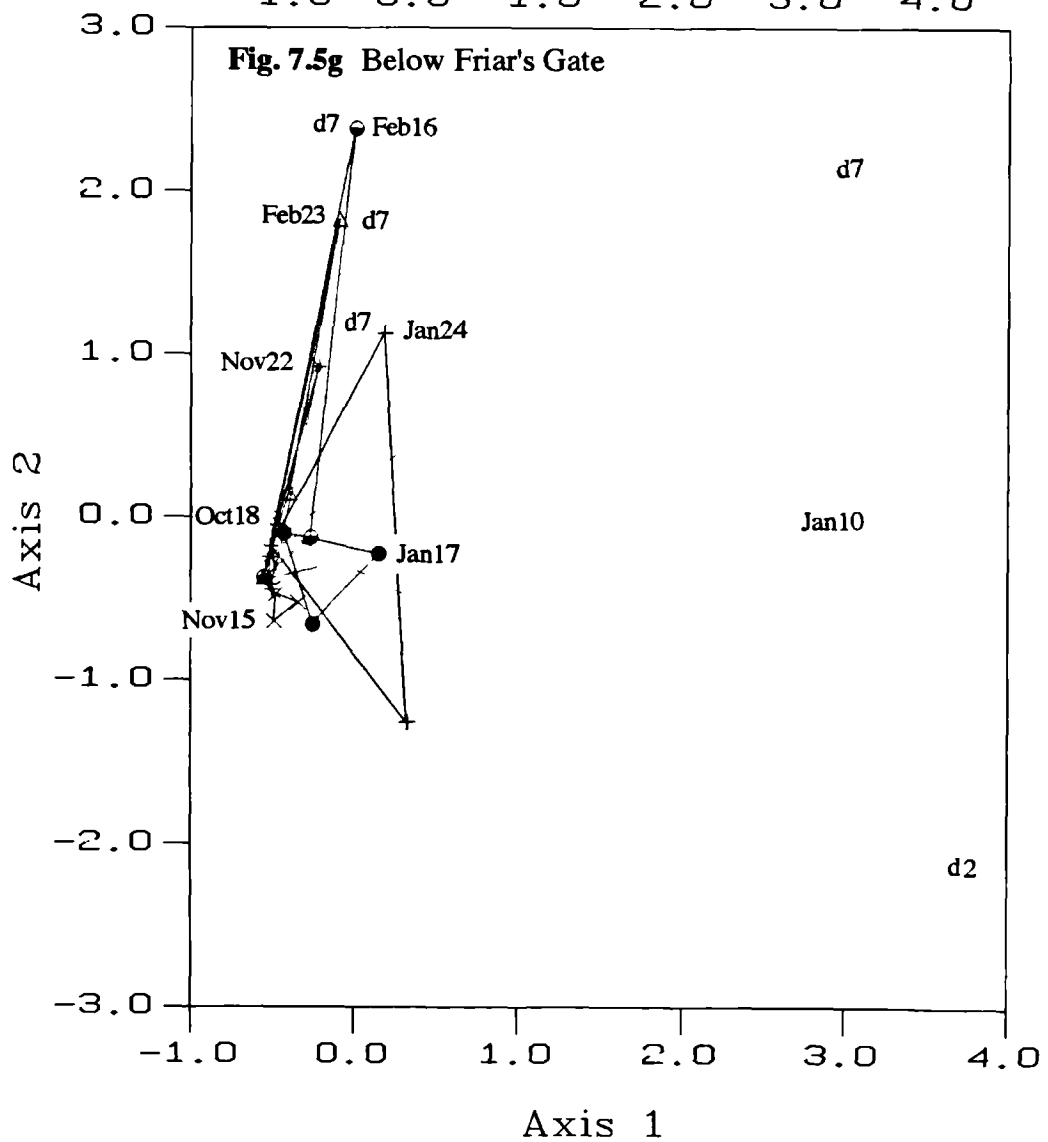
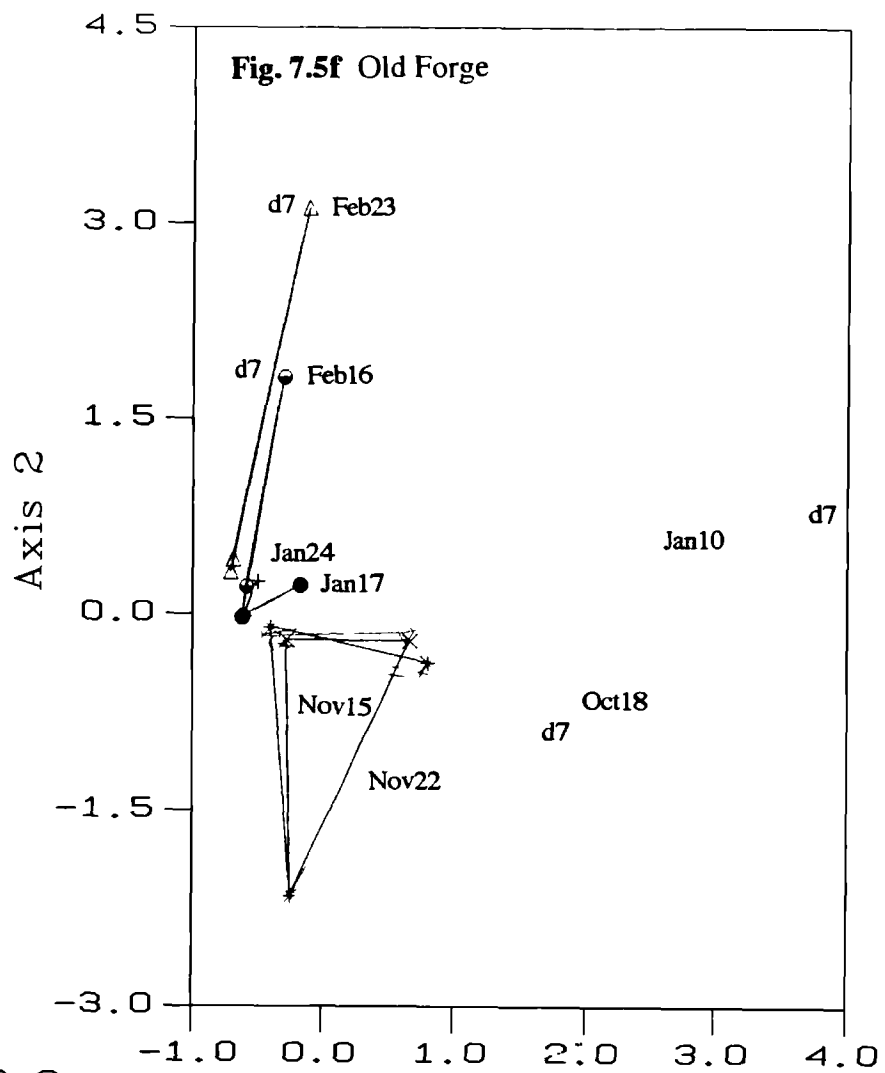


Fig. 7.5c Boringwheel Mill

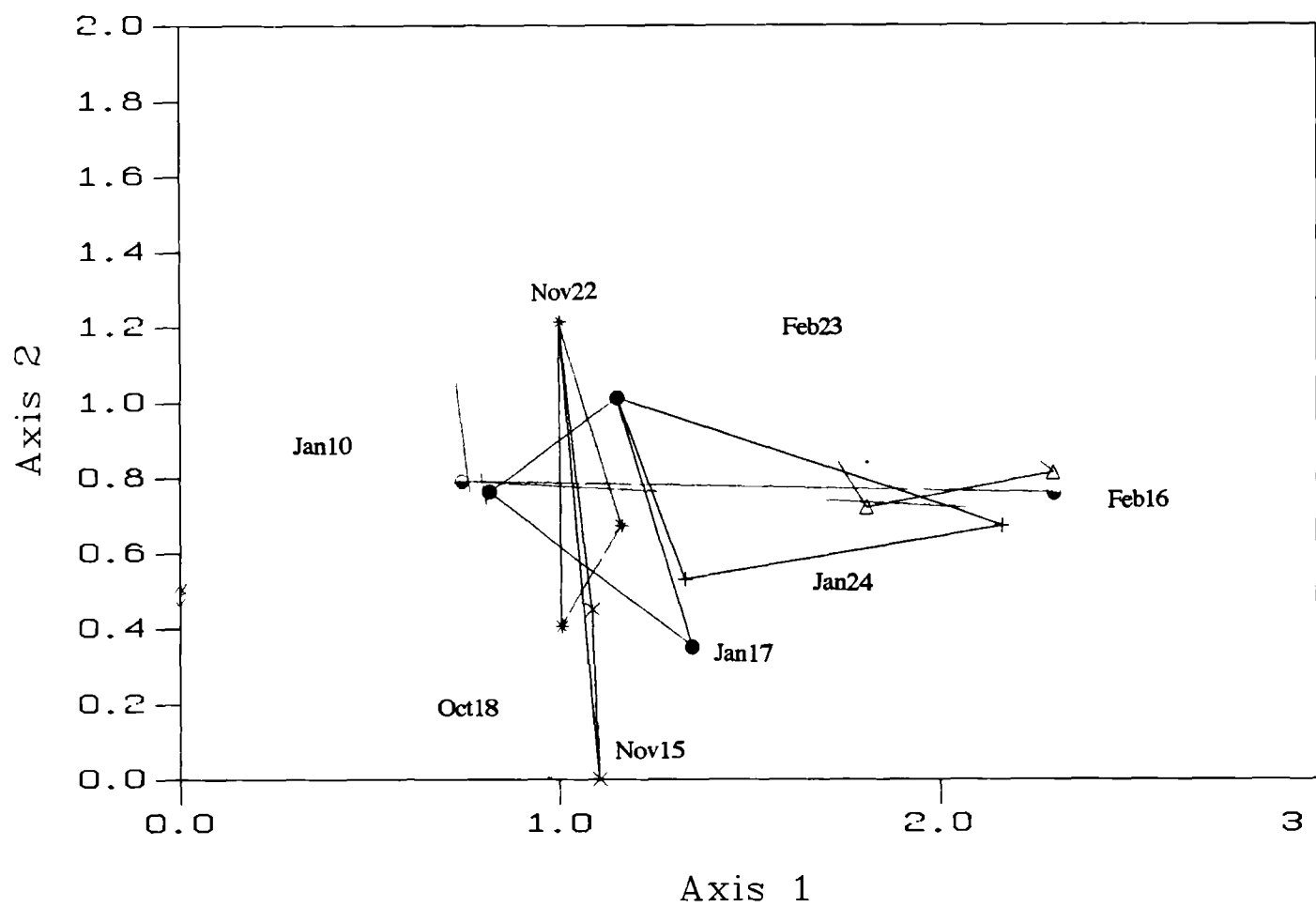


Fig. 7.5d Marsh Green

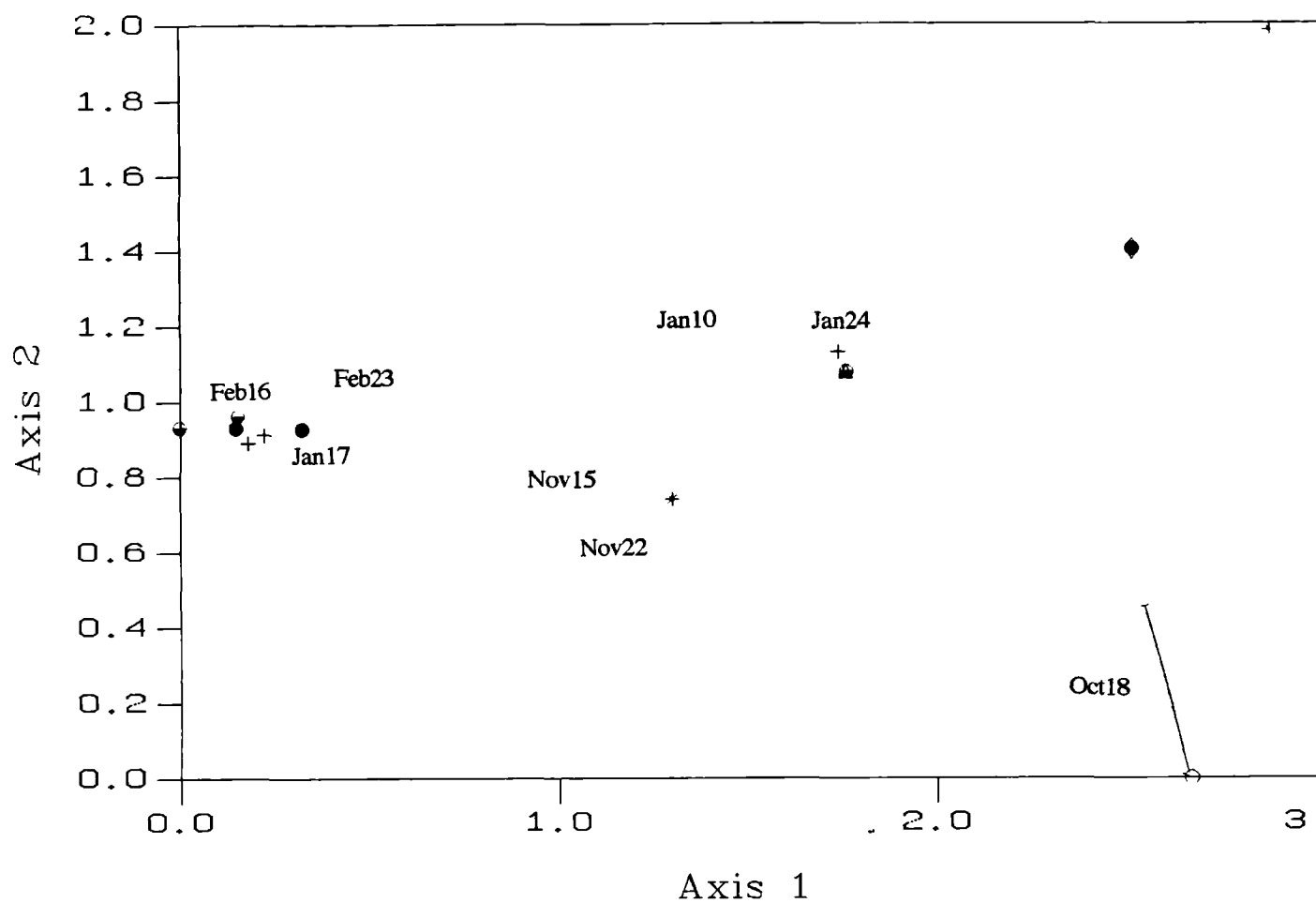
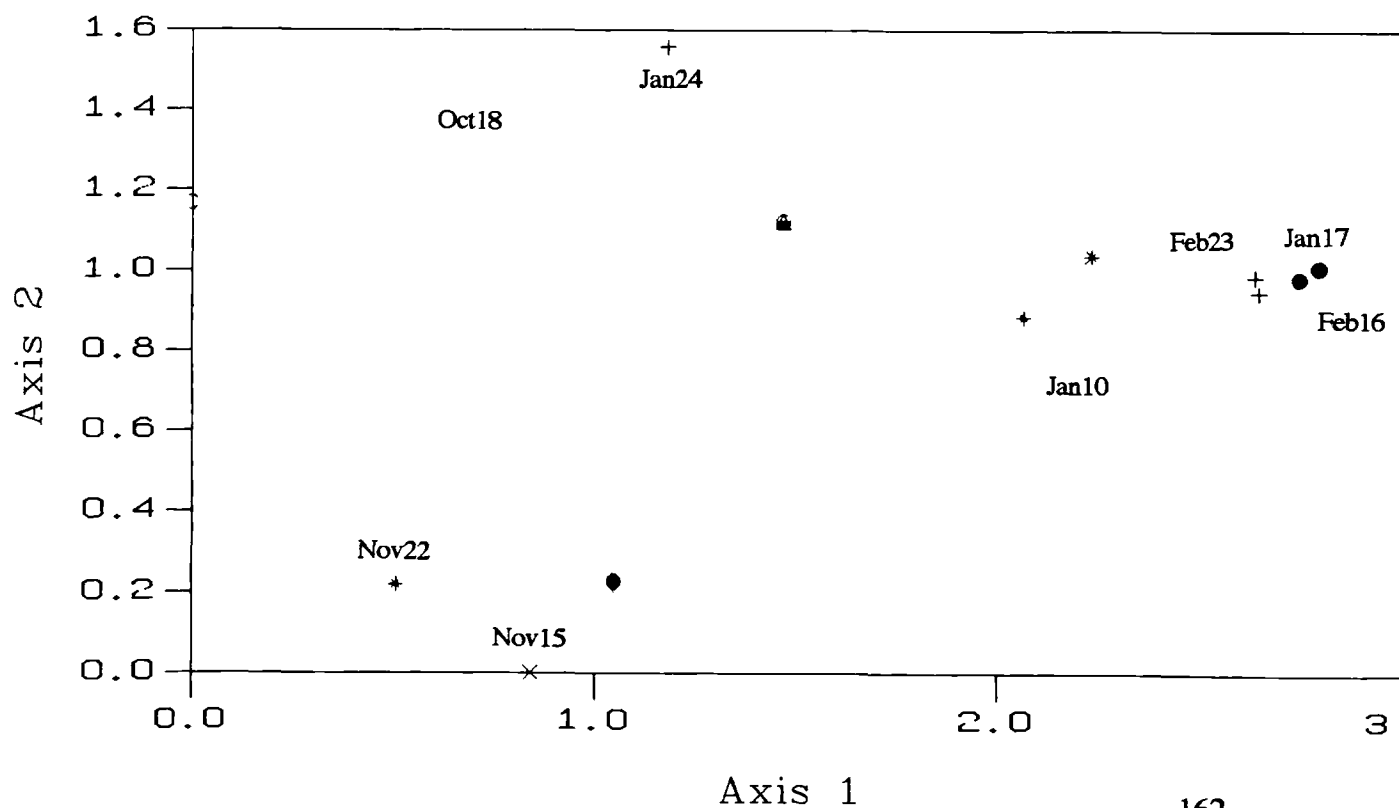


Fig. 7.5e Withyham



biplot represent the Surbers, Cage 2 and Cage 7 communities on the 18th October. Hulls are only drawn around the individual weeks if a high proportion of the weeks are closely clustered.

Broadstone Stream (Fig. 7.5a) and Batt's Bridge (Fig. 7.5b) both showed fast colonisation rates at low discharge, and a slower rate at medium and high discharge. The points for the 10th January are close together in the Broadstone biplot; this was the first high flow event in the Ashdown Forest since the previous spring, and the closeness of the points is more likely to reflect a depletion of the background fauna rather than a rapid increase in abundances in cages.

Old Forge (OF) (Fig. 7.5f) and Below Friar's Gate (BFG) (Fig. 7.5g) both showed similar patterns. The Surber and Day 2 cages were very similar, both being very species poor, but Day 7 cages in both streams have much higher abundances, which on the biplots is indicated by Day 7 cages being very different (further away) from Day 2 cages and Surbers. This higher abundance in Day 7 cages was especially apparent at high flow. Only Day 7 cages (d7) are indicated on the figures to avoid overcrowding.

The benthic community at Boringwheel Mill (Fig. 7.5c) showed a greater difference between Surbers and cages than the streams mentioned previously, indicating a slower return to pre-disturbance levels. No distinct pattern was seen with discharge. Although recolonisation was not rapid at Boringwheel Mill, it was faster than at Marsh Green (Fig. 7.5d) and Withyham (Fig. 7.5e). These streams showed large differences between the organisms in the cages and those in the background Surbers at all discharges. Hence, discharge does not seem to make much difference to the communities in these streams.

7.3.iv. Single date, all sites

Each week (discharge) was analysed independently for all sites to give an idea of between-site variations at different discharges, i.e. how one specific discharge

affects colonisation rates at each site. Thus, this type of analysis investigates the effects of discharge on colonisation rates between sites.

All gradient lengths were greater than 2 in the DCAs for the 'single date, all sites' data set (Table 7.9). Eigenvalues were high for all dates, indicating good separation of species data, and most sites had about 30% of species variation explained by the first two axes.

Table 7.9. DCA percentage transformed data, single date, all sites.

	Axis 1	Axis 2	Axis 3	Axis 4
October 18th, 1995:				
Eigenvalues	0.712	0.435	0.155	0.066
Gradient lengths	4.393	2.932	1.832	1.654
Cumulative % variation of species data	19.9	32.0	36.3	38.2
Sum of all unconstrained Eigenvalues				3.585
November 15th, 1995:				
Eigenvalues	0.624	0.274	0.106	0.061
Gradient lengths	3.585	2.321	2.092	1.832
Cumulative % variation of species data	19.3	27.8	31.0	32.9
Sum of all unconstrained Eigenvalues				3.236
November 22nd, 1995:				
Eigenvalues	0.614	0.350	0.191	0.096
Gradient lengths	3.628	2.473	2.380	1.643
Cumulative % variation of species data	17.5	27.5	32.9	35.7
Sum of all unconstrained Eigenvalues				3.506
January 10th, 1996:				
Eigenvalues	0.637	0.450	0.146	0.067
Gradient lengths	3.381	3.397	1.912	1.768
Cumulative % variation of species data	21.1	36.1	41.0	43.2
Sum of all unconstrained Eigenvalues				3.011
January 17th, 1996:				
Eigenvalues	0.592	0.318	0.159	0.058
Gradient lengths	3.291	2.558	2.333	1.370
Cumulative % variation of species data	20.6	31.7	37.3	39.3
Sum of all unconstrained Eigenvalues				2.868
January 24th, 1996:				
Eigenvalues	0.549	0.310	0.155	0.053
Gradient lengths	3.101	2.419	2.345	2.446
Cumulative % variation of species data	19.5	30.5	35.9	37.8
Sum of all unconstrained Eigenvalues				2.820
February 16th, 1996:				
Eigenvalues	0.587	0.420	0.165	0.059
Gradient lengths	3.315	2.861	1.732	2.100
Cumulative % variation of species data	18.9	32.4	37.6	39.5
Sum of all unconstrained Eigenvalues				3.111
February 23rd, 1996:				
Eigenvalues	0.516	0.253	0.127	0.053
Gradient lengths	3.039	1.752	1.714	1.648
Cumulative % variation of species data	20.5	30.6	35.6	37.7
Sum of all unconstrained Eigenvalues				2.515

Each individual biplot in this analysis shows the results for a single week (discharge) (Fig. 7.6a-h). The clusters are single sites, and each point represents either a Surber, Day 2 or day 7 Cage in each site for that week. Thus, for example, there is a cluster of half-filled red circles to the far left on the 18th October biplot (Fig 7.6a). This cluster consists of Surber and Cage communities for Broadstone Stream on 18th October.

All streams showed fast colonisation rates on 18th October (the points within the clusters are very close together). On the two other low flow occasions (Figs. 7.6b-c) Withyham and Marsh Green showed lower colonisation rates than the other sites. For both streams, the points furthest away in the clusters are the Surbers, so Day 2 assemblages were very similar to Day 7 assemblages, which in turn were both very different from background assemblages.

At medium discharge (Figs. 7.6d-f) Marsh Green and Withyham again consistently had slow colonisation rates, but then Batt's Bridge (Figs. 7.6d-f) and Boringwheel Mill (Figs. 7.6e-f) also showed slower colonisation rates. Broadstone Stream, Old Forge and Below Friar's Gate all still had fast colonisation rates.

Patterns were quite different on the two high flow occasions. January 10th was the first real spate experienced in the Forest since the previous spring. Most of the streams on this date are tightly clustered (Fig. 7.6g), indicating great similarity between cages and Surbers, although Withyham, Marsh Green and Boringwheel Mill show some dissimilarities. This tight clustering means either that cages were similar to Surbers (colonisation rates were fast), or that Surbers were similar to cages (background communities were impoverished). Examining the raw data it seems that background communities were impoverished only after the spate, so colonisation rates were in fact high. Colonisation rates on the second high flow occasion were much the same as at medium flow; they were slow in Marsh Green, Withyham, Boringwheel Mill and Batt's Bridge, fast in Broadstone Stream and Old Forge, and fast-medium fast in Below Friar's Gate.

Fig. 7.6. DCA ordination biplots of a) October 18th; b) November 15th; c) November 22nd; d) January 17th; e) January 24th; f) February 16th; g) January 10th; h) February 23rd. Single dates, all sites. Data were percentage transformed.

Year	Date	Discharge at Broadstone (m ³ s ⁻¹)	Flow
1995	October 18th	0.0031	'low'
	November 15th	0.0052	'low'
	November 22nd	0.0080	'low'
1996	January 10th	0.1553	'high'
	January 17th	0.0125	'medium'
	January 24th	0.0152	'medium'
	February 16th	0.0147	'medium'
	February 23rd	0.0607	'high'

Fig. 7.6a October 18th, 1995

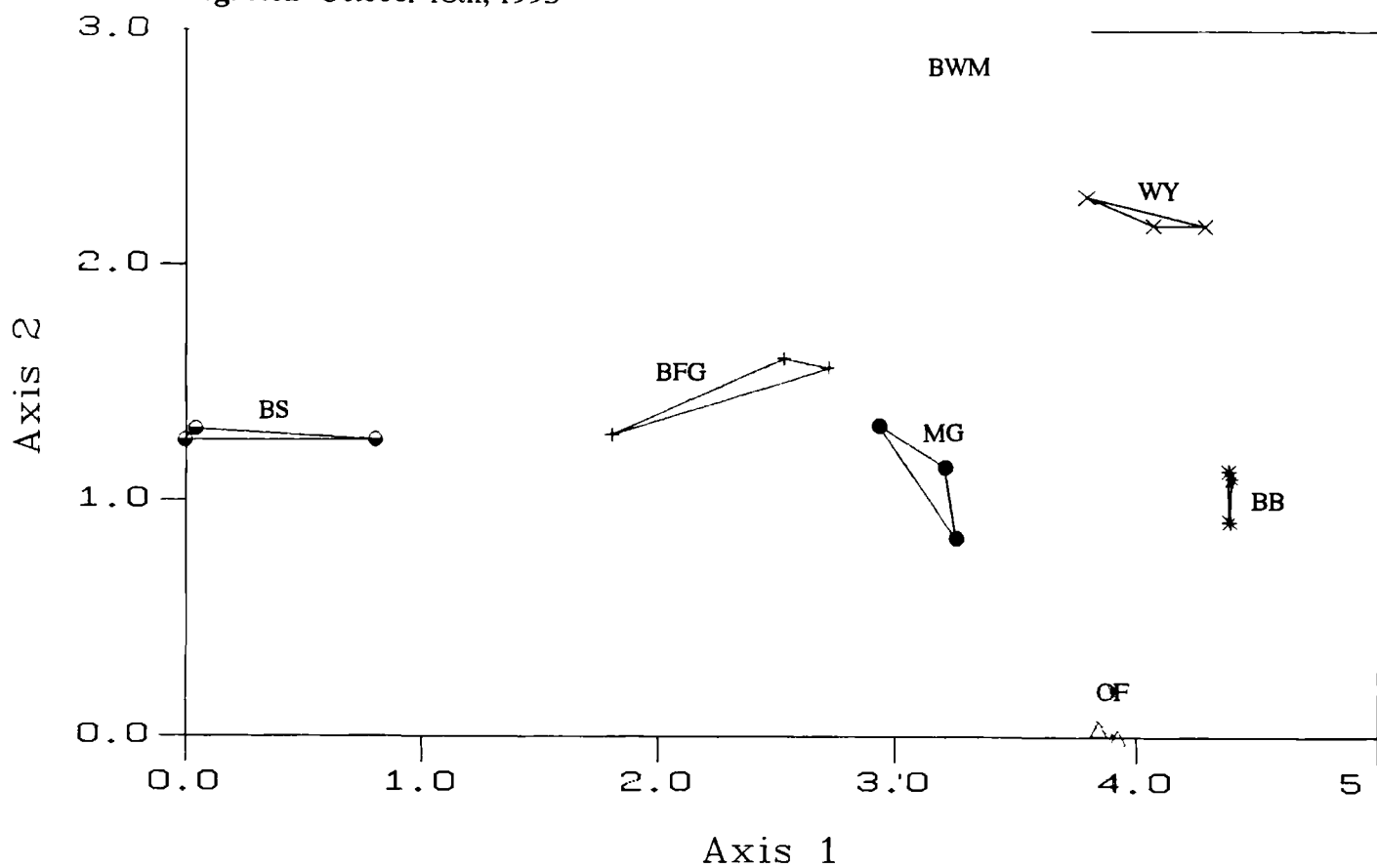


Fig. 7.6b November 15th, 1995

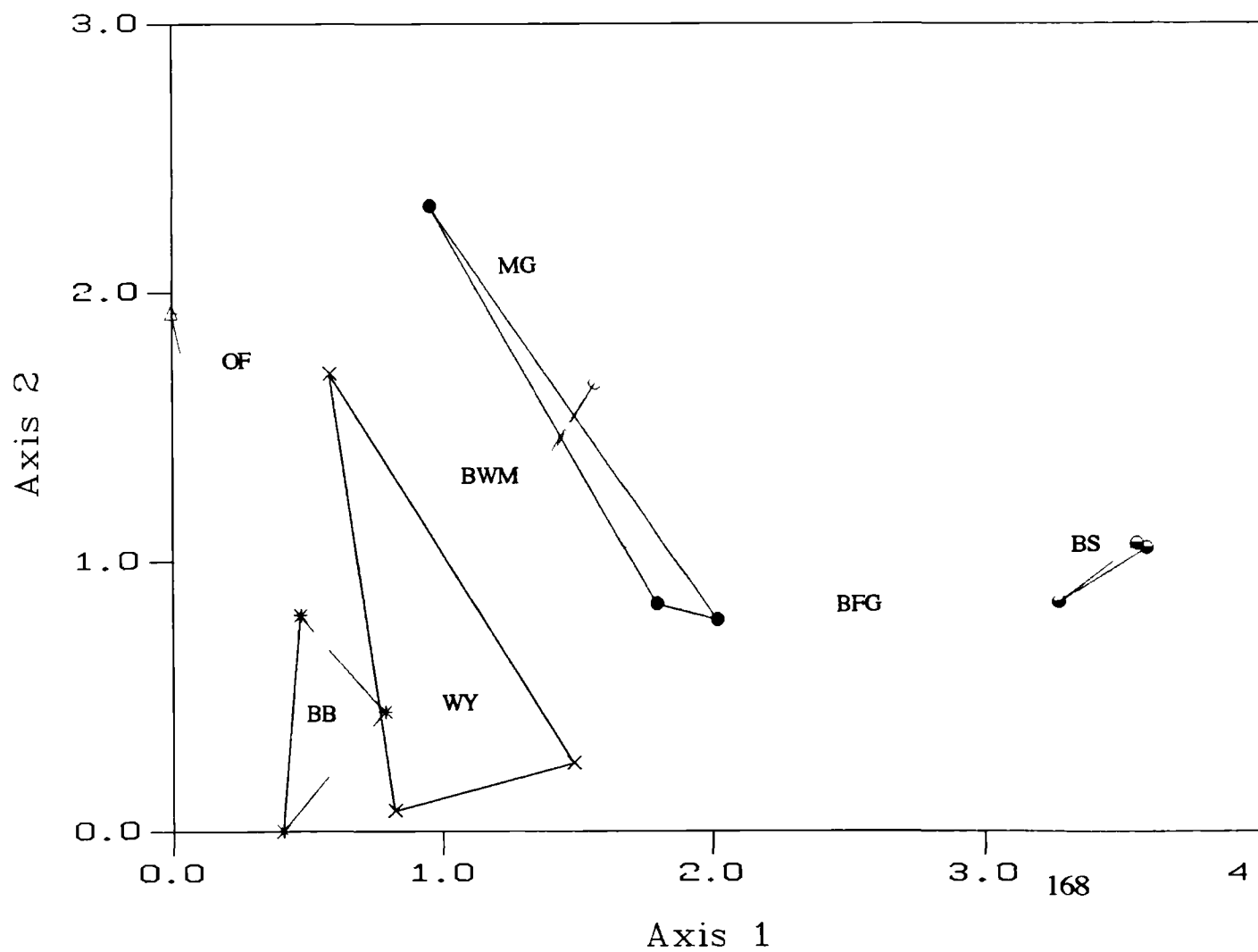


Fig. 7.6c November 22nd, 1995

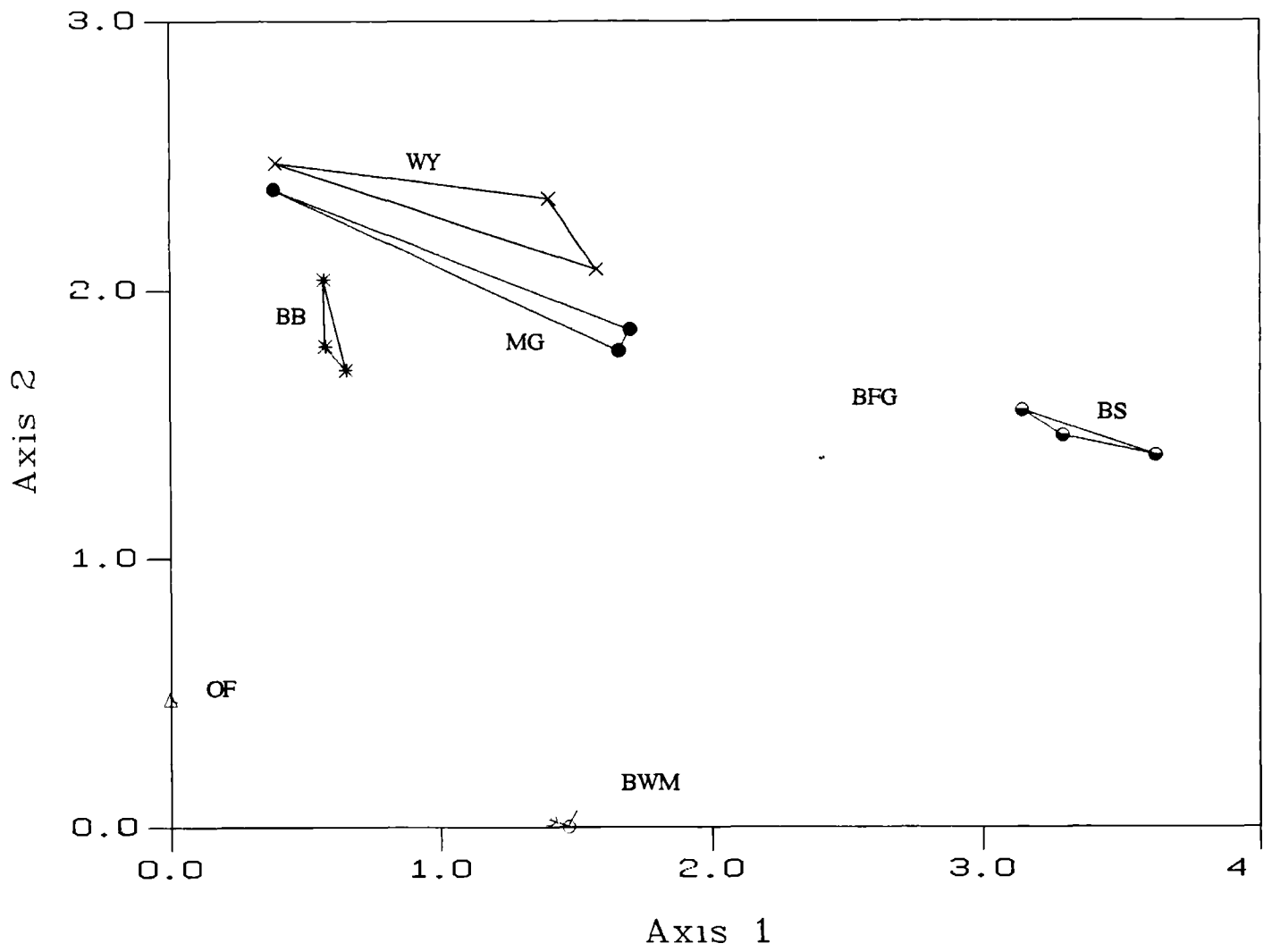
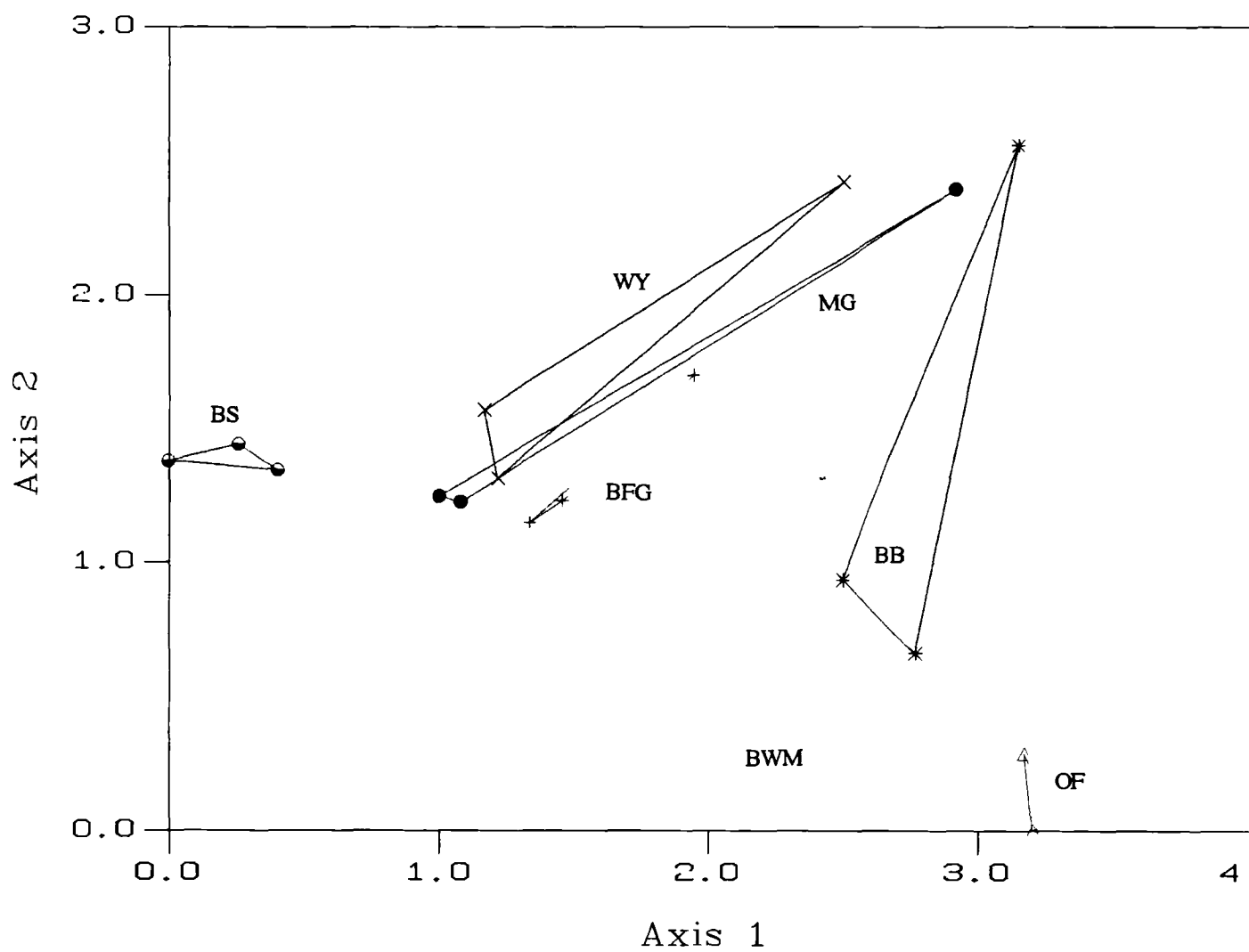


Fig. 7.6d January 17th, 1996



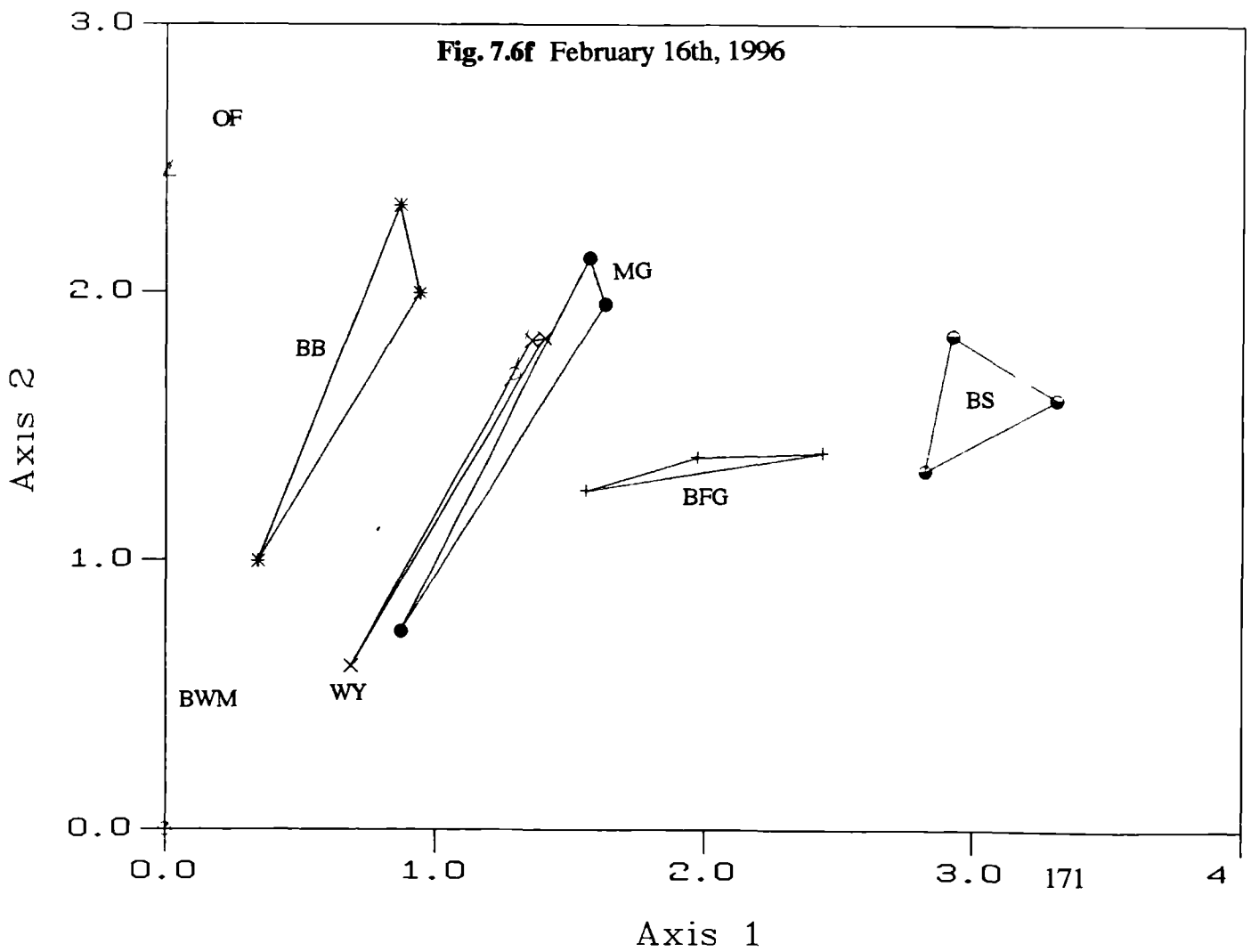
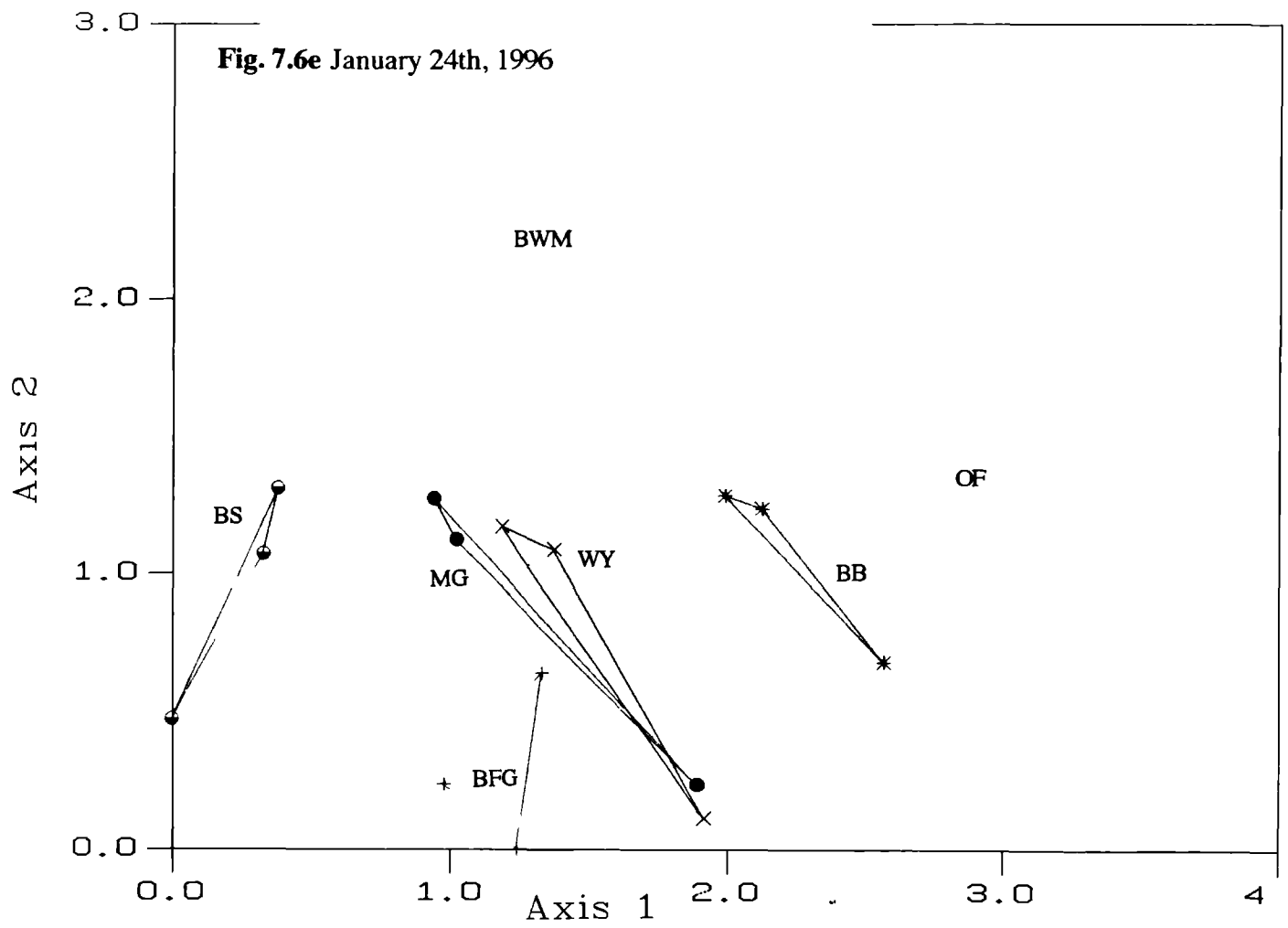


Fig. 7.6g January 10th, 1996

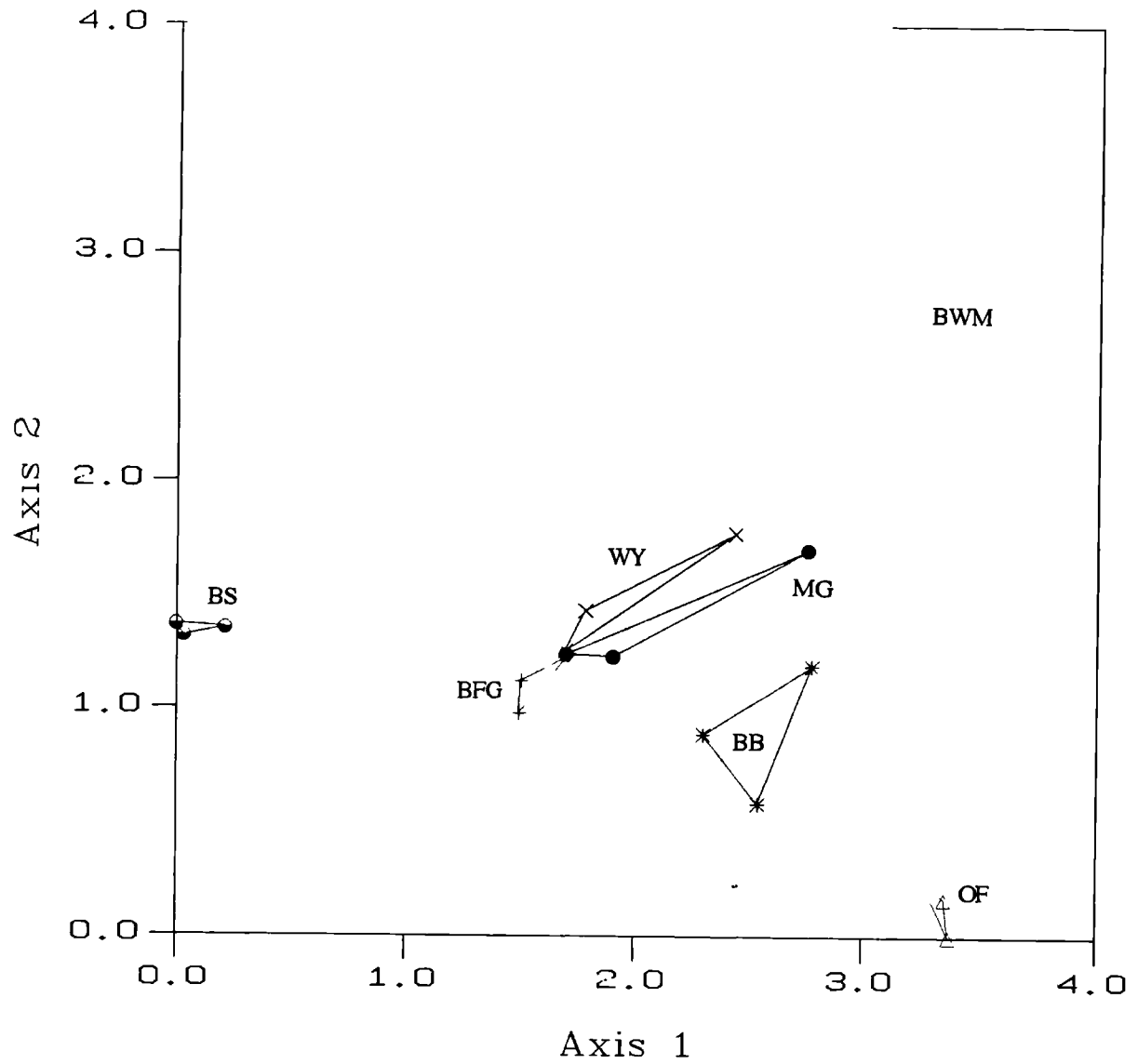
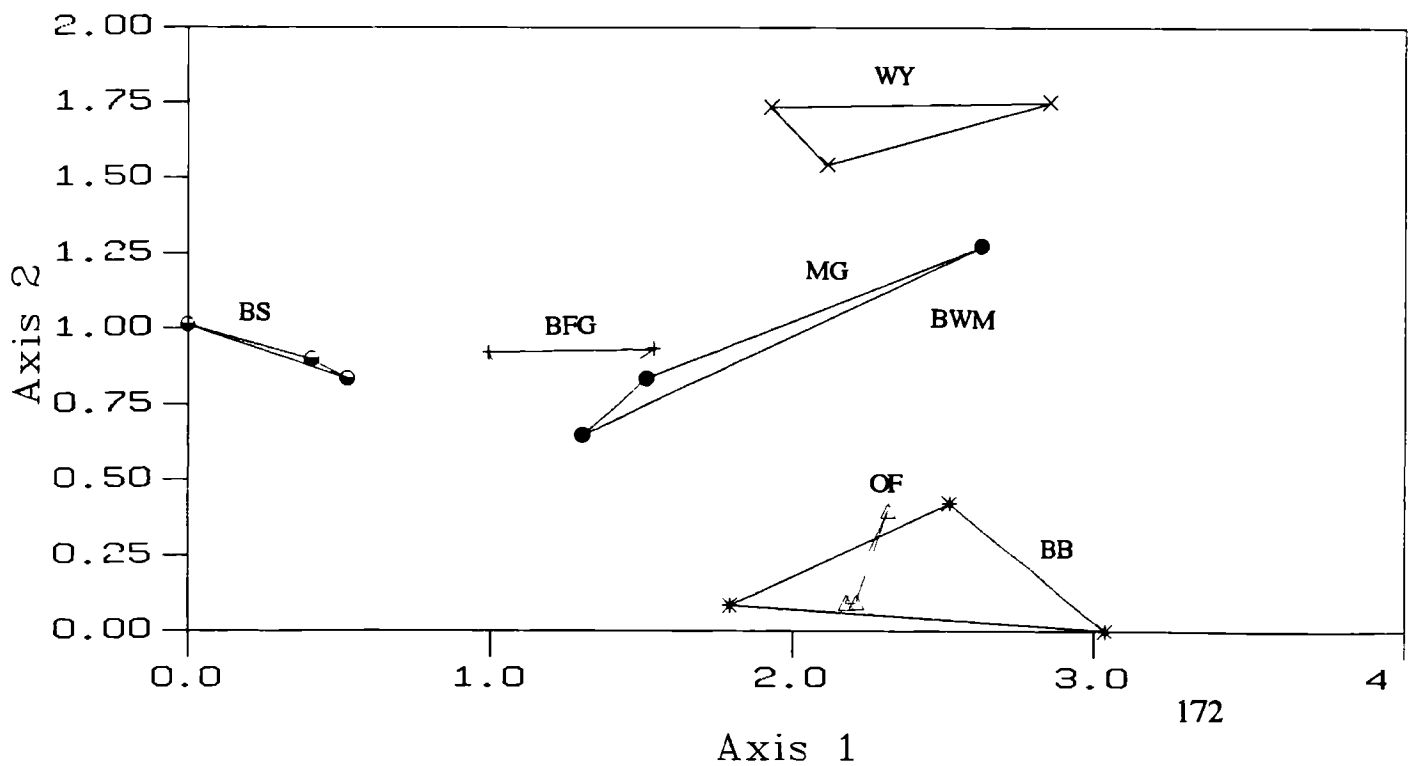


Fig. 7.6h February 23rd, 1996



7.3 v Mobility indices (colonisation) for both abundance and species richness

A regression of the mobility index on discharge is shown in Figs. 7.7 & 7.8. A mobility index of 0.69 ($\ln(1+1)$) indicates that abundances inside cages were equal to background levels, values above 0.69 indicate that cage abundances were higher than background levels. The y intercept of the lines indicate colonisation when discharge is negligible, while the slope is an indication of the susceptibility of the community to increasing discharges. The steeper the slope, the more susceptible the community is to changes in discharge. By comparing the slopes and intercepts of the regression lines, different degrees of mobility and sensitivity to discharge can be detected between streams.

An Analysis of covariance showed a non-significant interaction term between site and discharge (Table 7.10), indicating homogeneity of slopes, i.e. that there was no significant difference between the responses to discharge between streams. Although these were non-significant for both abundance and species richness, the

Table 7.10. Analysis of covariance (ANCOVA) for homogeneity of slopes and intercepts between \ln mobility indices for species richness and abundance, sites and log discharge. (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

	SS	DF	MS	F	P
Cage 7: species richness					
site*discharge	0.079	6	0.013	0.631	0.705
site	0.882	6	0.147	7.349	***
discharge	0.219	1	0.219	10.956	**
Cage 7: abundance					
site*discharge	2.387	6	0.398	2.028	0.083
site	12.601	6	2.100	9.484	***
discharge	8.629	1	8.629	38.966	***

term was only just non-significant for the abundance data, and the pattern suggested by Fig. 7.7 suggests that the less disturbed streams (Old Forge, Broadstone Stream and Below Friar's Gate) have a progressively greater response (steeper slopes) to discharge than the more disturbed streams.

Fig. 7.7. Logarithmic relationship between index of mobility (ratio of numbers of colonists to benthic density: $\ln(\text{mobility index} + 1)$) and maximum weekly discharge ($\log(\text{discharge} + 1)$) for the communities in a) Old Forge, b) Broadstone Stream, c) Below Friar's Gate, d) Marsh Green, e) Boringwheel Mill, f) Withyham, and g) Batt's Bridge.

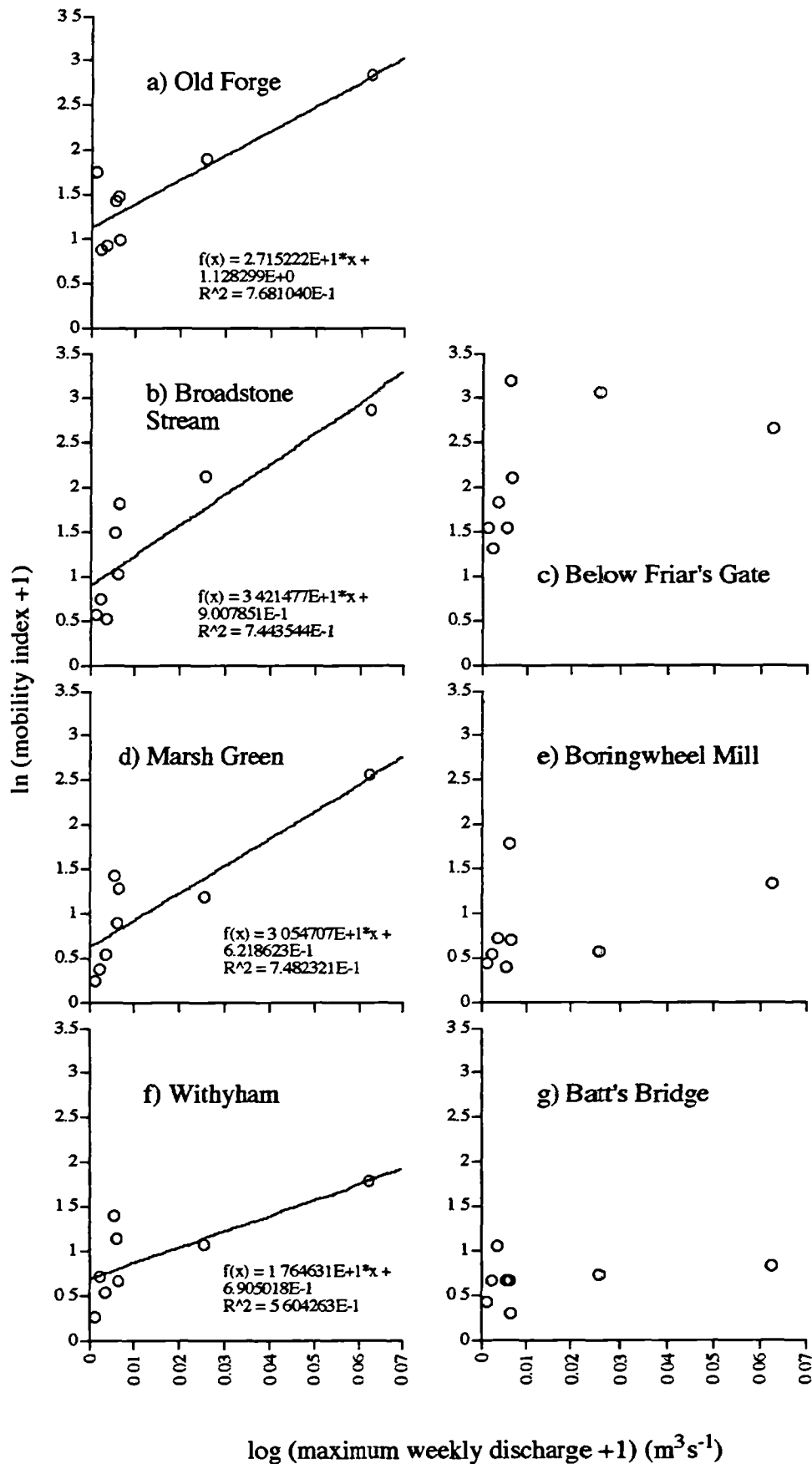
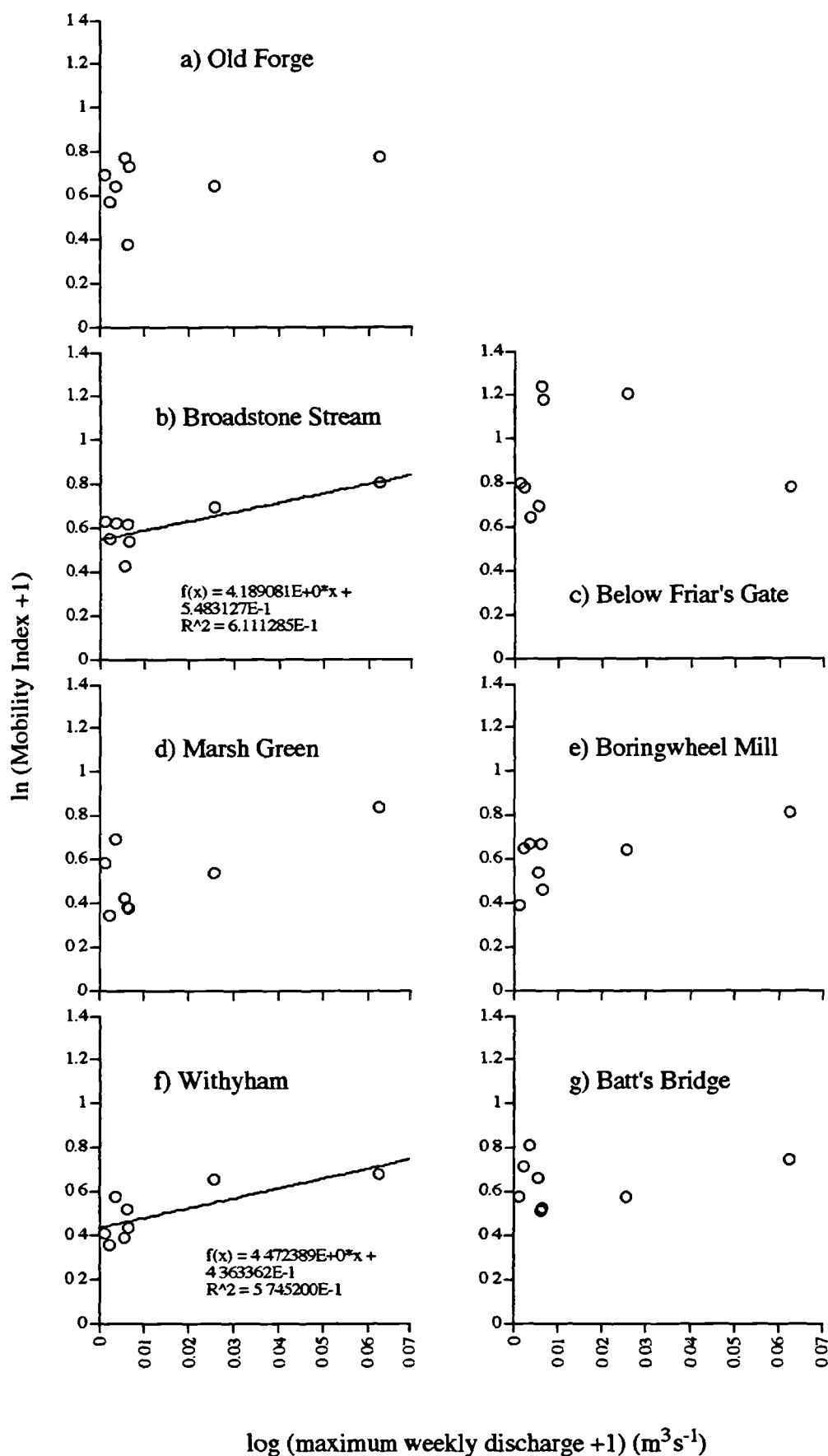


Fig. 7.8. Logarithmic relationship between index of mobility (ratio of numbers of species of colonists to benthic species richness: $\ln(\text{mobility index} + 1)$) and maximum weekly discharge ($\log(\text{discharge} + 1)$) for the communities in a) Old Forge, b) Broadstone Stream, c) Below Friar's Gate, d) Marsh Green, e) Boringwheel Mill, f) Withyham and g) Batt's Bridge.



The significant results for site and discharge in the ANCOVA suggest that colonisation rates did increase with discharge (slope is greater than zero) for all sites equally, and that the elevation of the sites (intercept) along the mobility axis are significantly different; colonisation rates varied between streams both in terms of abundance and species richness.

Tukey's *post hoc* test calculates pairwise probabilities. A significant result indicates that the two sites compared have different colonisation rates at low discharge (intercepts). The species richness results show that Below Friar's Gate was

Table 7.11. Tukey's *post hoc* pairwise test of similarities of elevations (=intercepts) for mobility indices calculated from a) species richness and b) abundance. (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

a) Species Richness	BS	OF	BFG	MG	WY	BWM
Broadstone	1					
Old Forge	0.998	1				
Below Friar's Gate	**	**	1			
Marsh Green	0.869	0.543	***	1		
Withyham	0.727	0.374	***	1.000	1	
Boringwheel Mill	1.000	0.994	***	0.907	0.783	1
Batt's Bridge	0.999	1.000	**	0.629	0.454	0.998
b) Abundance	BB	OF	BWM	BS	MG	WY
Batt's Bridge	1					
Old Forge	*	1				
Boringwheel Mill	0.997	0.054	1			
Broadstone	*	0.998	0.182	1		
Marsh Green	0.626	0.461	0.927	0.796	1	
Withyham	0.890	0.207	0.996	0.494	0.999	1
Below Friar's Gate	***	0.121	***	*	***	***

different to all other sites, but no other differences between sites were shown (Table 7.11). Abundances were different between Below Friar's Gate and all sites but Old Forge, but also between Batt's Bridge and Old Forge, and between Batt's Bridge and Broadstone Stream.

7.3.vi. Summary

Overall colonisation results are summarised in Table 7.12. Mobility index analyses revealed that there was no significant difference between the ways communities in the different sites reacted to increases in discharge. Both the multivariate analyses and the graphical representation of mobility indices indicated, however, that communities in Old Forge, Below Friar's Gate and Broadstone Stream responded to fluctuating discharge, although the results showed contradicting responses. DCAs suggested a faster colonisation at low flows, while the mobility indices indicated faster colonisation at fast flow. Batt's Bridge, Boringwheel Mill, Marsh Green and Withyham did not show a strong response to increased discharge.

Background fluctuations in the benthic communities were high in Marsh Green and Withyham, low in Broadstone Stream and Boringwheel Mill, and low to medium in Batt's Bridge, Old Forge and Below Friar's Gate.

Colonisation rates were slow in Marsh Green and Withyham, fast in Broadstone Stream, Old Forge and Below Friar's Gate, and medium to low in Boringwheel Mill. The very high colonisation rates at Below Friar's Gate, throughout the experimental period, were caused in part by the fact that more organisms colonised cages than were found outside; this suggested cages were being preferentially colonised.

The placement of the seven streams on a habitat templet with axes of disturbance frequency and refugium availability is shown in Table 7.13. Generally fast colonisation rates are found towards the lower left of the templet; these are streams of low to medium disturbance regimes with a high to medium refugium

Table 7.12. Summary of results of multivariate and mobility index analyses for the seven sites included in the experiment. All rates are relative to each other. (ns) in the mobility index descriptions indicates that the regression was not significant.

Site	Background community fluctuations	Colonisation rates compared to other sites (i.e. between-site)	Effect of discharge <u>within</u> sites	Mobility Index (abundance) at intercept (baseline mobility)	Mobility Index (species richness) at intercept (baseline mobility)
Marsh Green	high	slow	none	medium-high	medium-low (ns)
Withyham	high	slow	none	medium-low	medium-low
Broadstone Stream	low	fast	faster at low	high	medium
Boringwheel Mill	low	medium	none	low (ns)	medium (ns)
Batt's Bridge	low-medium	fast + slow	faster at low	low (ns)	medium-high (ns)
Old Forge	low-medium	fast	faster at medium	fast	medium-high (ns)
Below Friar's Gate	medium	fast	faster at low	high (ns)	high (ns)

availability. At high flows especially, these fast colonisation rates are partly caused by higher abundances inside cages compared to outside. Sites with a low refugium availability and low to medium disturbance frequency (lower right in Table 7.13) show consistently slow colonisation rates, with little or no effect of discharge.

Table 7.13. The placement of the seven streams in relation to disturbance frequency and refugium availability. BWM = Boringwheel Mill, BB = Batt's Bridge, BS = Broadstone Stream, OF = Old Forge, MG = Marsh Green, BFG = Below Friar's Gate, WY = Withyham.

	Type I	Type II	Type III
High disturbance frequency		BWM: Medium to low colonisation rates. Independent of discharge. Medium mobility indices.	(BB: Fast colonisation rates at low discharge only. Low mobility indices.)
Medium disturbance frequency	BS: Fast colonisation rates. Faster at low discharge. High mobility indices.	OF: Fast colonisation rates. Some effect of discharge. High mobility indices.	MG: Consistently slow colonisation rates. Independent of discharge. Medium to low mobility indices.
Low disturbance frequency		BFG: Fast colonisation rates. Some effect of discharge. High mobility indices at all discharges.	WY: Consistently slow colonisation rates. Independent of discharge. Low mobility indices.

Boringwheel Mill, the site with intermediate refugium availability and high disturbance frequency, showed intermediate colonisation rates while discharge had little effect on colonisation rates. The placement of Batt's Bridge on the templet was uncertain. This was the only non-gravel site included in the experiment and refugium

availability estimated by Lamouroux *et al*'s model (1992) predicted it to have the highest refugium availability of all the original twenty-two streams investigated (Chapter 4). Due to this uncertainty it is not included in the final discussion.

In summary then; refugium availability seems to be of overall importance in determining colonisation rates of the benthic macroinvertebrates during this study. Sites with high refugium availability generally had fast colonisation rates, and sites with low refugium availability had slow colonisation rates. At intermediate refugium availability the disturbance regime seems important; where communities are subjected to frequent disturbances, fluctuations in discharge were unimportant and colonisation rates were consistently intermediate. In streams where communities seldom or occasionally are subjected to disturbances, fluctuations in discharge were of some importance, but colonisation rates were generally fast.

7.4 Discussion

In frequently disturbed habitats high mobility is thought to be an adaptive trait (Pianka, 1970; Townsend & Hildrew, 1994). Organisms may actively or passively enter refugia during or before flow events and disperse from them afterwards, leading to rapid recolonisation. High mobility may therefore only be favoured where there are many refugia, and the results of this experiment support that view.

Refugium availability seems to be of primary importance in determining colonisation rates, and disturbance frequency only of secondary importance. Increases in discharge led to slightly faster (although not significant) rates of colonisation in the less frequently disturbed streams with more refugia. Their communities were also generally more mobile at low discharges, indicating that mobility was not entirely a response to disturbance. Biotic interactions are thought to be more important in relatively undisturbed streams, and it is possible that the high mobility is a reflection of this. Competing for resources or avoiding predation is likely to demand some degree of mobility in a patchy environment.

Marchant *et al* (1991) found that relative rates of colonisation (colonists in relation to background) did not vary with flooding regime, but absolute rates (total numbers) were directly proportional to the numbers of individuals and taxa, i.e. the more organisms available to colonise, the more will colonise.

Lake & Schreiber (1990) also found that streams with high species richness and densities had high absolute colonisation rates, but they found the opposite relationship with relative colonisation rates; slow relative colonisation rates were found in their species rich downstream sites, and a rapidly colonising, opportunistic fauna was found in their upland streams. These results are supported by the present study, where species poor upstream sites generally had faster colonisation rates than species rich downstream sites.. However, Lake & Schreiber's upstream sites were much further upstream and more disturbed than their downstream sites. The species poor upstream sites in this study are less disturbed than the species rich downstream sites. Thus, the species richness/ abundance pattern is confirmed by my results, but the disturbance pattern is not consistent.

Differences in abundances and species richness between sites were controlled for by calculating mobility indices and also by using percentage data in the multivariate analyses. The most species poor sites with the lowest abundances had the highest colonisation rates and, although relative rates were used, it cannot be ruled out that these faster rates were not in some way connected to the availability of colonists. However, Boringwheel Mill, the most species rich site, had intermediate colonisation rates, suggesting that species richness was not directly related to colonisation rates.

Below Friar's Gate had very low species richness and abundance, and levels of these within cages were often much higher than outside. This suggested cages were being colonised preferentially. Possible explanations are that the flow was reduced inside the cages by leaves trapped on the upstream side at high flow creating artificial flow refugia. Research has shown that in streams where refugia are naturally abundant, they are used more readily by the invertebrates inhabiting the streams (Winterbottom *et al*, 1997). Preferential colonisation could also be caused by the

substratum being stabilised, or the stones inside the cages being cleaned regularly. This site is very iron-rich (Plate 2.1, page 21), and it is possible that organisms may preferentially colonise substratum particles free of iron bacteria.

Finally, the difference between the community responses on the two high flow occasions highlight the problem of between- or even within-site comparisons at different times. Communities responded much more dramatically to the first high flow disturbance, which followed a long period of low flow, than the second event which followed not long after the first. Communities had had a longer period of uninterrupted succession when subjected to the first disturbance than was the case for the second disturbance. Comparisons with other community responses to disturbances must include an indication of time since last disturbance.

CHAPTER 8: General discussion.

It is a basic aim of ecology to understand the relationship between a bewildering variety of organisms and the environment in which they are found. Natural habitats are spatially and temporally heterogeneous (Sousa, 1984) and exert powerful influences over the distribution, interactions and adaptations of organisms (Southwood, 1977, 1988). Southwood's Habitat Templet (1977, 1988) potentially provides the framework on which hypotheses and predictions can be based. Since the hypothesis was generated it has found support by workers in many fields (e.g. Grime, 1977, 1979; Greenslade, 1983; Sibly & Calow, 1985; Hildrew & Townsend, 1987; Poff & Ward, 1990). In lotic ecology disturbance theory (Pickett & White, 1985; Resh *et al*, 1988; Townsend, 1989; Reice *et al*, 1990; Hildrew & Giller, 1994) and the role of refugia (Lancaster & Hildrew, 1993; Robertson *et al*, 1995; Palmer *et al*, 1995; Lancaster & Belyea, 1997) have received increasing attention in the last decade, and the use of these two environmental variables have been proposed as suitable templet axes (Townsend, 1989; Poff & Ward, 1990; Scarsbrook & Townsend, 1993; Hildrew & Townsend, 1994; Townsend *et al*, 1997). In this study I aimed to test the habitat templet theory in a high number of streams in close geographic proximity in the Ashdown Forest, East Sussex, using refugium availability and disturbance frequency as axis labels.

Disturbance frequency was estimated using two different techniques and a comparison made. Substratum movement at different levels of discharge was measured using tracer particles, and the number of days a year 50% of the stream bed was in movement could be estimated. This was compared to the traditional method of Wolman (1954) where 100 substratum particles are picked at random and the diameters measured. Bed stability can be estimated from the degree of imbrication or interaction of particles (Sear, 1992). Both techniques were reliable and showed very similar estimates, and a disturbance frequency was estimated for each stream. Although some streams were estimated to have very high disturbance frequencies

(Boringwheel Mill), there was generally very little variation among coarse gravel bed streams with most streams being disturbed between 3 and 26 days per year.

Instream flow refugia have been shown potentially to be very important in 'buffering' the effect of disturbance (Lancaster *et al*, 1996; Schmid-Araya, 1994, 1994; Winterbottom *et al*, 1997a). Refugium availability was estimated from shear stress frequency distributions using FST hemispheres (Statzner & Müller, 1989) and by modelling (Lamouroux *et al*, 1992). The modelled shear stress frequency distributions were consistently underestimated at low flows compared to shear stress measured by the hemispheres. It was, therefore, decided to use refugium availability as measured empirically by the hemispheres (stream 'Types').

A long-term sampling regime provided useful information on the persistence of communities in the Forest. More frequently disturbed streams with lower refugium availability were predicted to be less persistent than undisturbed streams with high refugium availability. A comparison of sites revealed that all sites were approximately equally persistent, and no pattern was found with disturbance frequency or refugium availability. If communities in streams of contrasting disturbance regimes are equally persistent, then some degree of adaptation to the habitat is to be expected.

Extensive literature reviews (Statzner *et al*, 1994; Statzner *et al*, 1997) were assessed to obtain traits for as many of the species as possible in the Ashdown Forest. Species traits were compared to environmental variables using multivariate statistics. Only weak patterns were shown, although one of the traits that was significantly different between sites was poor mobility. It is believed that the concept of 'trade-offs' between traits and the constant problem faced by ecologists of scale (e.g. Hildrew & Townsend, 1994; Statzner *et al*, 1997) are the causes of this poor correlation.

The mobility trait that was found to be weakly significant in the previous Chapter was examined more closely. It is generally believed that frequently disturbed streams will have a higher proportion of mobile species to enable rapid recolonisation. Extensive field experiments using colonisation cages revealed that there was indeed a difference between streams, but that communities in less disturbed

streams were actually more mobile than those in disturbed streams. Mobility was also found to be associated with refugium availability suggesting that unless organisms have somewhere to disperse from, mobility may not necessarily be an advantageous trait.

Finally I return to the question of scale, so frequently discussed by lotic ecologists (e.g. Frissell *et al*, 1986; Statzner *et al*, 1997). Large scale/ long term approaches showed few or no differences between sites in this study. pH (or the variables highly correlated with it: temperature and distance from source) seems to determine the overall community structure of the sites. Disturbance frequency and refugium availability did not significantly contribute to explaining variation in species at this scale. A small scale/ short term approach, however, revealed differences in mobility. These findings are surprising and begs the question "Why are organisms more mobile in less disturbed habitats?" Experimental research on species interactions show differences in mobility between species that are related to predation (Lancaster, 1996), food availability (Kohler, 1984, 1985), or refugium use (Winterbottom *et al*, 1997a; Lancaster *et al*, 1996). The present study suggests that high mobility is more likely to be associated with biotic interactions than as a disturbance response. Certainly this is a topic that would benefit from further research.

Southwood's vision of an 'ecological Periodic Table' is probably optimistic, considering the bewildering variety of nature. It does, however, provide a promising framework on which to base questions, predictions and testable hypotheses.

Invertebrate drift and longitudinal transport processes in streams

Jill Lancaster, Alan G. Hildrew, and Charlotte Gjerlov

Abstract: Benthic macroinvertebrates were disturbed from stream substrata and caught in drift nets at various distances downstream. Four experiments were carried out at several discharges in each of four streams with contrasting hydraulic transport characteristics. The numbers of all invertebrates and of Plecoptera in the water column at each distance were fit to a negative exponential function. The channel with the highest mean velocity had the lowest return rate (β). In any one channel, β decreased with increasing velocity; this relationship approximated a power function, with stream-specific slope corresponding to channel hydraulics. The stream with a high fraction of dead zones had high β values that varied little with velocity; streams with fewer dead zones had lower β values that decreased with increased velocity. At any particular velocity, channel-specific depth and turbulence may account for different β values in streams with similar dead zones. The return rates of two stonefly families varied relative to one another, possibly owing to species-specific behavioural changes in response to current. In a low-velocity stream, Leuctridae had higher β values than Nemouridae; the rates were similar in a higher velocity stream. Our results are consistent with the view that the physical habitat influences the distance drifted by dislodged invertebrates.

Résumé : On a délogé des macro-invertébrés benthiques des substrats de cours d'eau, et on les a attrapés à l'aide de filets dérivants à diverses distances en aval. On a effectué quatre expériences, avec plusieurs débits, dans quatre cours d'eau à caractéristiques de transport hydraulique très différentes. On a ajusté dans une fonction exponentielle négative les valeurs obtenues à chaque distance pour tous les invertébrés et les Plécoptères dans la colonne d'eau. Le chenal ayant la vitesse moyenne la plus élevée donnait le taux de capture (β) le plus faible. Dans tous les chenaux, β diminuait en raison inverse de la vitesse; ce rapport obéissait approximativement à une fonction de puissance et la pente propre à chaque cours d'eau correspondait aux caractéristiques hydrauliques du chenal. Le cours d'eau ayant la plus forte proportion de zones d'eaux mortes avait une forte valeur de β variant peu avec la vitesse du courant, alors que ceux ayant moins de zones mortes avaient une plus faible valeur de β , diminuant en rapport inverse avec la vitesse du courant. À une vitesse particulière, la profondeur et la turbulence propres au chenal peuvent expliquer les valeurs différentes de β dans les cours d'eau comportant des zones mortes semblables. Les taux de capture pour deux familles de perles présentaient une variation relative, peut-être à cause de changements de comportement propres à l'espèce en réponse au courant. Dans un cours d'eau lent, on notait des valeurs plus élevées de β chez les Leuctridés que chez les Némuridés, et des taux semblables dans un cours d'eau plus rapide. Nos résultats sont cohérents avec l'opinion selon laquelle l'habitat physique influence la distance de dérive des invertébrés délogés.

[Traduit par la Rédaction]

Introduction

The extra support provided by the physical medium underlies many of the differences between terrestrial and aquatic systems (e.g., Giller et al. 1994). Suspension of living organisms and their transport in water currents thus plays a major role in the population and community ecology of freshwater and marine habitats. This transport is particularly significant in the one way flow systems of streams and rivers, where transport

in water currents is inexorably downstream. This has led to questions about how populations of benthic invertebrates, and particularly phytoplankton, can persist in running waters because organisms risk eventual transport to possibly unsuitable downstream reaches (e.g., Waters 1972; Muller 1974, 1982; Reynolds 1988). It seems possible that density-independent losses owing to downstream transport could reduce population size and that the fitness of displaced individuals would be reduced. Hence, we would expect invertebrates to show a tendency to move upstream when not actually drifting (e.g., Soderstrom 1987) and (or) to reduce the lifetime distance drifted. The extent to which either of these can be achieved is partly determined by the physical habitat.

The tendency for invertebrates to be displaced downstream by the current depends on three factors: (i) the frequency of drift events during the aquatic life-span, (ii) the distance drifted per event, and (iii) the length of aquatic life. The first two of these factors are influenced by direct interactions between organisms and the physical habitat, which itself consists of a complex of interacting factors. Firstly river discharge and its fluctuations are an obvious source of disturbance, and peaks

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Table 1. Physical characteristics of the four study streams.

Stream	Geographical coordinates	Mean annual pH	Mean width (m)	Mean depth (cm)	Discharge (m ³ s ⁻¹)		
					Mean daily min	Mean daily max.	Inst. max
Ashdown Forest							
Broadstone Stream ^a	0°03'00"E, 51°04'30"N	5.2	1.38	14.2	0.001	0.129	0.223
Lone Oak	0°04'00"E, 51°04'36"N	4.8	1.55	12.3	0.001	na	0.188
Galloway							
Green Burn ^b	4°22'25"W, 55°04'40"N	5.8	1.88	20.0	0.001	1.49	3.41
Dargall Lane ^b	4°25'00"W, 55°04'30"N	5.4	2.75	24.5	0.002	1.70	4.66

Note: Data are from Lancaster and Hildrew (1993). Inst. instantaneous.

^a1991–1992 discharge data from the National Rivers Authority Southern Region.

^b1985–1990 discharge data from the Solway River Purification Board.

in flow may scour individuals from the stream bed (Anderson and Lehmkuhl 1968; Poff and Ward 1991). Secondly, substratum stability may exacerbate or ameliorate flow disturbances. Flow events during which the substratum moves will be associated with high drift rates (Cobb et al. 1992). A third aspect of the physical habitat, that of water velocity and the heterogeneity and complexity of the velocity structure of the water column, may be particularly important in determining the distance animals drift per event (e.g., Elliott 1971; Ciborowski 1983). It is this last interaction, between physical habitat and drift distance, that is the focus of the present paper.

Although the net direction of flow in streams is always downhill, flow patterns are complex and particles in the water column do not all travel at the same rate. One method of characterizing channel hydraulics examines the longitudinal transport of solutes. The time it takes a solute to flush out of a reach depends on the complexity of flow and is influenced, in part, by how much water is held in transient storage or hydraulic dead zones. These are places within the stream channel that are not part of the bulk flow, but where some form of mixing or exchange occurs with the bulk flow. They are usually located in stream margins, turbulent eddies, wakes around roughness elements (e.g., boulders, logs), and reverse flows associated with pools and bends. Such dead zones provide opportunities for drifting invertebrates to regain the substrate, in addition to more obvious opportunities such as washing up against obstructions. Elliott (1971) noted that drift distances are influenced by the morphological characteristics of streams but did not test the idea explicitly. Transient storage models that describe solute transport and the abundance of hydraulic dead zones in a reach have clear practical applications and are well known to hydrologists (e.g., Bengala and Walters 1983; Wallis et al. 1989). More recently, they have been applied to problems in stream ecology, for example as models to characterize the abundance of flow refugia for river phytoplankton (Reynolds et al. 1991; Reynolds and Glaister 1993) and for benthic macroinvertebrates (Lancaster and Hildrew 1993) and to estimate nutrient storage, uptake, transport, and lateral inflow (Klem and Jackman 1992; D'Angelo et al. 1993). These models may also be useful predictors of invertebrate transport, and that is the subject of this investigation.

In this study, we used manipulative field experiments to examine (i) whether the distances invertebrates drift and the rate at which they return to the substratum reflect the hydraulic transport properties of different stream channels and (ii) whether the nature of the relationship between return rate and

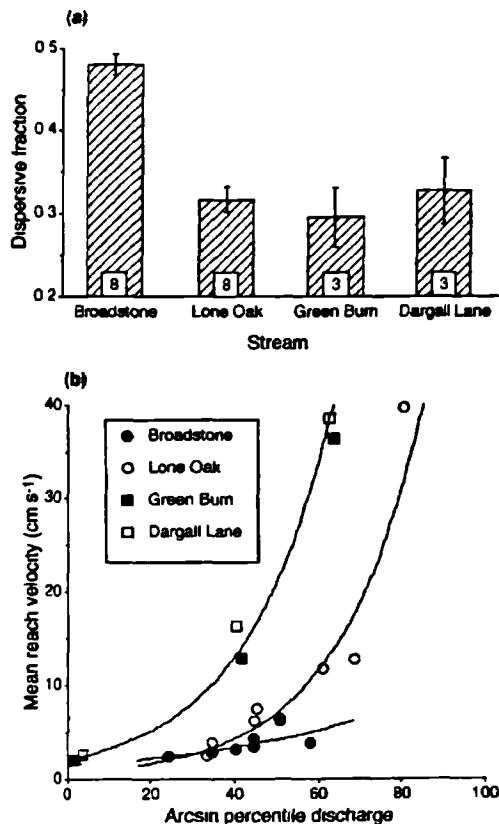
mean water velocity varies among channels. We predicted low drift distances (and high return rates) of entrained animals in channels with low mean velocities and a high proportion of hydraulic dead zones. Conversely, drifting animals should travel further where mean velocities are high and dead zone fractions low. The relationship between return rate and current velocity should be similar among streams with similar fractions of water in hydraulic dead zones.

Study sites

Experiments were carried out in four stream channels that differed in hydraulic character (Table 1): two lowland streams in the Ashdown Forest, East Sussex, southeast England, and two upland streams in Galloway, southwest Scotland. The English sites, Broadstone Stream and Lone Oak, are small first-order streams draining acid heath and some mixed woodland. They are geographically close together (3.5 km) and have similar water chemistry and species composition (Townsend et al. 1983; Hildrew et al. 1984). The Scottish stream sites are typically torrential upland streams with moorland catchments (Dargall Lane) or partially forested (conifers) catchments (Green Burn). They are close together (3.0 km) and have similar water chemistry (Solway River Purification Board, unpublished data) and similar species composition.

In a previous study, we characterized longitudinal transport processes in these streams, over a range of discharges, using solute dilution experiments and we applied transient storage models to the data (Lancaster and Hildrew 1993). The aggregated dead zone model (ADZ) (Beer and Young 1983; Young and Wallis 1986; Wallis et al. 1989) summarizes the effect of all dispersive processes and hydraulic dead zones in any length of stream channel. It uses an empirical, curve-fitting procedure based on time series analysis and models river discharge as two fractions, one actively flowing and one nonflowing or dead. The dispersive fraction is an estimate of the proportion of the total reach volume occupied by dead zones. Figure 1a shows the mean dispersive fraction of the four study streams, and it does not vary with discharge (Wallis et al. 1989; Lancaster and Hildrew 1993). Other hydraulic parameters that may influence invertebrate drift distances do vary with discharge, for example reach velocity. Figure 1b shows the mean reach velocity, as determined by solute tracer experiments (Lancaster and Hildrew 1993) in each stream as a function of discharge. Discharge has been presented as a percentile of the annual discharge frequency distribution to correct for

Fig. 1. Hydraulic transport characteristics of the four study streams. (a) Proportion of the total reach volume occupied by dead zones (dispersive fraction) (mean \pm 1 SE); numbers at the bottom of each bar indicate the number of experiments per stream. Redrawn from Lancaster and Hildrew (1993). (b) Relationship between mean reach velocity, as determined by solute tracer experiments (Lancaster and Hildrew 1993), and percentile discharge after arcsin transformation (0 = base flow; 100 = maximal discharge per annum). Exponential curves have been fit to the data for each stream; values for the two Scottish sites (Dargall Lane and Green Burn) are similar so a single curve has been drawn.



differences in stream size and hence on the x axis, 0 represents base flow whereas 100 represents maximal discharge. Not surprisingly, velocity increases with discharge in all of the streams but there are distinct patterns among the streams.

The hydraulic patterns illustrated in Fig. 1 allowed us to make specific predictions about invertebrate drift in our four streams. The likelihood of entrained animals being transported out of a reach was expected to be lowest in Broadstone Stream because it has the highest dispersive fraction (the greatest proportion of hydraulic dead zones) and the lowest reach velocity. Conversely, animals were expected to drift furthest in Green Burn and Dargall Lane, as they both have low dispersive fractions and similar, steep patterns of velocity with discharge. Invertebrate transport in Lone Oak should be intermediate be-

tween these extremes; its dispersive fraction is similar to that of Green Burn and Dargall Lane, but it has a lower mean reach velocity at any common percentile discharge. At any common velocity, the return rate of drifting animals should be similar among the three streams with similar dispersive fractions (Lone Oak, Dargall Lane, Green Burn) but should be greater in Broadstone Stream.

Methods

Experimental design

Field experiments were used to determine the transport distances and return rates of benthic macroinvertebrates. Animals were entrained in the water column by artificially disturbing the substratum (see below) and were then caught in a drift net downstream. Diel periodicity in drift behaviour is well known and the vulnerability of some species to flow varies accordingly (Campbell 1985; Larkin and McKone 1985; Lancaster 1992). We minimized this possible confounding factor by carrying out all experiments in the daytime. Four experiments were carried out in each of the four streams at different discharges (see Table 5) using one of two experimental designs: design A for small streams (Broadstone Stream, Lone Oak) and design B for larger channels (Dargall Lane, Green Burn). There are practical and analytical pros and cons associated with the two designs, but they provide similar numerical estimates of drift rates, as described at the end of this section.

In design A, a large rectangular drift net (31 \times 51 cm mouth, 330- μ m mesh) was placed in midchannel, flush to the substratum at the downstream end of the experimental reach (approximately 100 m). At a predetermined distance upstream, we entrained benthic invertebrates in the flow by shuffling across the stream channel and kicking the substratum, as uniformly as possible, along a band approximately 30 cm wide. This disturbance technique has been used previously in similar studies (McLay 1970; Larkin and McKone 1985). After a set period of time, all animals caught in the net were collected and preserved immediately. The drift net was then moved to a point upstream of the previous disturbance, and the whole process was repeated. A total of 25 disturbances were created in each experiment, with five replicates at each of five distances upstream of the net (0.5, 1, 2, 4, 8 m) in a randomly selected order. Drifting invertebrates were collected for 10 min after each disturbance at a distance of 4 m or more, 5 min at 2 m or less. Shorter times for short distances were used to reduce the total experimental time. We assumed that the plume of drifting invertebrates had passed the 2-m mark after 5 min, a minimal speed of 1.67 cm s⁻¹ that was considerably lower than the lowest mean velocity of 10 cm s⁻¹. At very high discharge (Lone Oak, April 5, 1993, 0.295 m³ s⁻¹), it was necessary to shorten these time intervals to avoid clogging the net. Background drift rates were estimated from five replicate drift samples collected on the same day over known periods of time, but without substratum disturbances. These background samples were collected within the experimental reach and inserted at random into the series of disturbance samples (see above). The volume of water filtered by the net during each sample collection was estimated from the cross-sectional area of water passing through the net mouth and mean velocity. Three measurements of the velocity at mid water column were taken in the net mouth and averaged over 10–20 s, using a bucket-wheel velocity meter (5 cm diameter) fitted with a photo-fibre-optic sensor.

In design B, benthic macroinvertebrates were entrained in the flow using the disturbance technique described above. Animals were collected simultaneously at six distances downstream (1, 2, 3, 5, 8, 12 m) in paired small drift nets with a circular mouth (50-cm² mouth, 330 μ m mesh) placed randomly across the channel, at mid water column, and left for 10 min. The volume of water filtered by each net was estimated from the cross-sectional area of the net and velocity at the net mouth

measured using the meter described above. Each experiment consisted of five replicate trials carried out in successive upstream reaches of the stream.

For both experimental designs, stream discharge was estimated three to five times each field day by measuring channel width, water depth, and mid column velocity at five points across the channel. Mean stream velocity was estimated from 10–20 mid-column velocity measurements at two pace intervals.

In the laboratory, animals were sorted and identified to species level when possible.

Data analysis

The data were calculated as the total number of animals in the drift at each distance from the disturbance in the entire stream over the whole time interval. Time intervals varied among distances in design A, so drift numbers were corrected for differences in background drift, as measured empirically on the same day:

$$N_x = Q \left(\frac{N'_x}{Q_x} - B \right)$$

where N_x is the total number of animals in drift at distance X , N'_x is the number caught in the drift net at distance X , Q_x is the discharge of the net at distance X ($\text{m}^3 \cdot \text{s}^{-1}$), Q is stream discharge ($\text{m}^3 \cdot \text{s}^{-1}$), t is the time interval over which drift was collected (s), and B is the background drift rate (number $\cdot \text{m}^{-3} \cdot \text{s}^{-1}$). In design B, the numbers of animals caught in downstream nets may be underestimates of the actual number drifting, owing to the removal of some animals from the drift by more upstream nets. Data were corrected for this dilution effect by increasing the catch by a factor related to the notional volume of water filtered by nets upstream:

$$N_x = N'_x \frac{Q}{Q_x} \prod_{i=1}^{x-1} \frac{Q}{Q - Q_i}$$

Notation is as above, except N_x is the sum of animals caught in the two paired nets at each distance and Q_x is the sum of discharges of the same pair. It was not necessary to correct for background drift in design B because the time interval for sampling was identical in all cases.

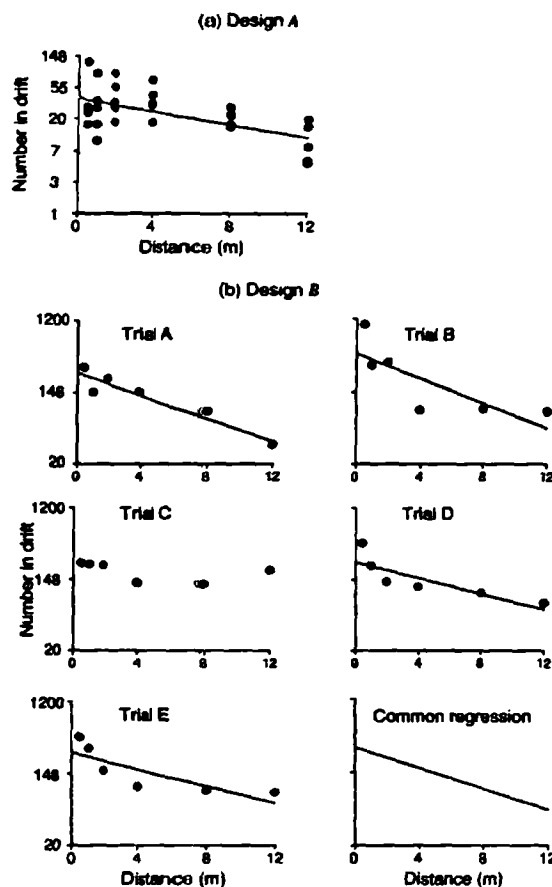
A negative exponential relationship was fit to the data to describe the number of animals in the drift with respect to distance from the disturbance, as has been established in previous studies (e.g., McLay 1970, Elliott 1971, Larkin and McKone 1985, Allan and Feifarek 1989):

$$N = N_0 e^{\beta X} \text{ or } \ln(N) = \ln(N_0) - \beta X$$

where N_0 is the number of animals entrained in the flow by the disturbance, X is the distance downstream of the disturbance (m), and β is the return rate, or settling coefficient (proportion $\cdot \text{m}^{-1}$). Note that in these equations we follow the notation of McLay (1970), Elliott (1971), Ciborowski (1983), Larkin and McKone (1985), Allan and Feifarek (1989), and others, except that return rate R is replaced with β to avoid confusion with R^2 , the coefficient of determination.

In design A, the data for each regression were analyzed by replicated regression (multiple values of Y for each X) according to Zar (1984). In design B, regression equations were calculated for each replicate trial. For each experiment, those trials in which there was a significant fit of the data to the line were tested for homogeneity of slopes using analysis of covariance (ANCOVA). These analyses are illustrated in Fig. 2 and Tables 2 and 3 by data collected on a single species of stonefly using the two protocols in the same stream at the same discharge. In the analysis of design A, the test of deviation from linearity (Table 2, line 1) was not significant. Therefore, the deviations MS and within distances MS were pooled to form the residual MS, $s_{Y \cdot X}$ (Table 2, line 3), and this was used as an estimate of the population variance (Zar 1984) to test for the goodness of fit (Table 2, line 2). Because the relationship is assumed to be linear, $s_{Y \cdot X}$ is the appropriate variance to use in the computation of standard

Fig. 2. Drift densities of the stonefly *Amphnemura sulcirostris* in relation to distance (downstream of a disturbance), during two experiments (designs A and B) carried out in Dargall Lane at the same discharge. Note that y axes are logarithmic. See Tables 2 and 3 for summary of statistical analyses. See text for further explanation of experimental designs.



errors associated with the slope, β , and the y intercept (Zar 1984). In the analysis of design B, trial C did not fit the regression model sufficiently well ($p > 0.05$, Table 3, line 1; Fig. 2), for reasons unknown, and was omitted from further analysis (similar omission of a trial occurred in only one other experiment). The slopes of the remaining four lines were all significantly different from 0. ANCOVA further indicated a significant linear relationship (Table 3, line 3) and the test for differences among slopes was not significant (Table 3, line 4), indicating that trials A, B, D, and E all provide estimates of the same population value of β . The common regression coefficient and its standard error were then calculated according to Zar (1984). Values for the y intercepts of each of trials A, B, D, and E were used to estimate the mean y intercept, and the associated errors were added in quadrature. The slope β represents the return rate or settling coefficient (proportion of animals returning to the substrate for every metre travelled) and the y intercept ($\ln(N_0)$ above) is the natural log of the number of animals entrained in the flow by the disturbance.

There are various practical and analytical pros and cons associated with the two experimental designs. However, they provide similar estimates of return rates, as illustrated in Fig. 2 and Tables 2 and 3.

Table 2. Summary of statistical analyses (linear regression with replication) used to describe drift distances of the stonefly *Amphinemura sulciatilis* in the design A experiment in Dargall Lane (see Fig. 2). The regression coefficients (mean \pm 1 SE) were as follows: β -0.104 ± 0.027 ; y intercept, 3.662 ± 0.167 ; $R^2 = 0.348$.

Line	Source	SS	df	MS	F	p
1	Among distances	7.078	5			
	Linear regression	5.598	1			
	Deviation from linearity	1.480	4	0.370	0.985	ns
	Within distances	9.018	24	0.376		
	Total	16.097	29			
2	Linear regression	5.598	1	5.598	14.93	<0.001
3	Residual	10.498	28	0.375		
	Total	16.097	29			

Note: See text for further explanation of experimental designs and statistical procedures and references to line numbers 1–3. R^2 refers to the coefficient of determination for statistical models, ns indicates $p > 0.05$.

Table 3. Summary of statistical analyses (linear regression and ANCOVA) used to describe drift distances of the stonefly *Amphinemura sulciatilis* in the design B experiment in Dargall Lane (see Fig. 2). Common regression coefficients (mean \pm 1 SE) were as follows: β , -0.106 ± 0.017 ; y intercept, 1.988 ± 0.105 .

Regression analysis for each replicate trial							
Line	Trial	R^2	Slope (β)	y intercept	df	F	p
1	A	0.903	-0.117 ± 0.005	5.545 ± 0.123	1,4	535.40	<0.001
	B	0.627	-0.137 ± 0.046	6.067 ± 0.412	1,4	7.701	<0.05
	C				1,4	1.129	ns
	D	0.704	-0.081 ± 0.029	5.487 ± 0.221	1,4	9.530	<0.05
	E	0.682	-0.089 ± 0.032	5.583 ± 0.249	1,4	8.597	<0.05

Results of ANCOVA for trials A, B, D, and E ($R^2 = 0.732$)

Line	Source	SS	df	MS	F	p
2	Trial	0.579	3	0.193	0.930	ns
3	Distance	8.133	1	8.133	32.210	<0.001
4	Trial \times distance	0.291	3	0.097	0.468	ns
	Error	3.319	16	0.207		

Note: Values for the slope and y intercept are given as the mean \pm 1 SE. See text for further explanation of experimental designs and statistical procedures and references to lines 1–4. R^2 refers to the coefficient of determination for statistical models, ns indicates $p > 0.05$.

Similar conclusions were drawn from comparisons of the two protocols using data for other species or species assemblages. Design B requires less time in the field, but it is practical only in large streams, whereas transport distances can be characterized in small streams using design A. Perhaps the greatest source of error in the data can be attributed to variations in the number of animals entrained in the flow by the artificial disturbances. Protocol A requires many such disturbance events and hence has smaller R^2 values. Higher R^2 values are obtained in design B, but it is more sensitive to other sources of variation that produce outliers. We are confident that both experimental designs were satisfactory for our objectives in the four streams examined. Any future applications of these techniques may favour one or the other technique, depending on the particular objectives and circumstances.

Results

Approximately 10 000 invertebrates (minimum 160 maximum >4000) were entrained in the drift by each disturbance event as estimated by y-axis intercepts of regression equations (see Table 5 below). The variability is probably attributable at least in part, to the patchy distribution of invertebrates

in streams. Individual species were not collected in sufficient numbers in all experiments to permit a species by species analysis, so our analysis is restricted to total invertebrates and the Plecoptera as a group. All four streams had broadly similar invertebrate communities and were dominated by the Plecoptera, mainly members of the Nemouridae and Leuctridae (Table 4). Broadstone Stream and Lone Oak had very similar assemblages in both autumn and spring, reflecting their close proximity and similar chemical character. The lower proportional representation of Plecoptera in Lone Oak in spring is attributable to a marked increase in the numbers of Simuliidae. Recalculated proportions excluding Simuliidae in spring were much closer to those in autumn: 0.25 for *Nemoura* spp. and 0.28 for *Leuctra nigra*. Green Burn and Dargall Lane also had similar assemblages, although *Brachyptera risi* occurred only in Green Burn, and there was virtually no difference in species relative abundances among experiments.

The negative exponential model of invertebrate drift provided a reasonable description of the data relating drift catches to distance travelled from the source of the disturbance (Fig. 2, Tables 5 and 6). Significant common regression equations

Table 4. Relative abundance of invertebrates in disturbance drift samples that made up $\geq 1\%$ of the total individuals

	Broadstone		Lone Oak		Green Burn	Dargall Lane
	Autumn	Spring	Autumn	Spring		
Plecoptera						
<i>Brachyptera risi</i> (Morton)					0.31	
<i>Protonemura meyeri</i> (Pictet)					0.06	0.08
<i>Amphnemura sulcicollis</i> (Stephens)					0.23	0.43
<i>Nemurella picteti</i> Klapalek	0.07	0.07				
<i>Nemoura</i> spp			0.27	0.19		
<i>Leuctra inermis</i> Kempny					0.12	0.01
<i>Leuctra hippopus</i> (Kempny)	0.09	0.06	0.07	0.01	0.01	0.09
<i>Leuctra nigra</i> Olivier	0.54	0.52	0.38	0.21		
<i>Isoperla grammatica</i> (Poda)					0.03	0.08
<i>Siphonoperla torrentium</i> (Pictet)			0.02	0.01	0.08	0.06
Megaloptera						
<i>Sialis fuliginosa</i> Pictet	0.03	0.03				
Trichoptera						
<i>Plectrocnemia conspersa</i> (Curtis)	0.04	0.04	0.08	0.09		0.02
Diptera						
Tipulidae			0.01	0.04		0.03
Simuliidae		0.02	0.02	0.25	0.07	0.03
Chironomidae	0.16	0.26	0.08	0.17	0.03	0.13
<i>N</i>	6367	2149	1919	4620	8909	2483

Note: Values for Green Burn and Dargall Lane are from all four experiments in early spring combined. Values for Broadstone Stream and Lone Oak are the average of two autumn and two spring experiments (see Table 5 for dates).

were fit to the total invertebrate and stonefly catches in all experiments. In the analysis of design A experiments (Broadstone Stream and Lone Oak), tests for deviation from linearity (e.g., Table 2, line 1) were nonsignificant in all cases, so the statistics summarized in Tables 5 and 6 represent the tests for goodness of fit only (e.g., Table 2, line 2). In design B experiments (Green Burn and Dargall Lane), results of the ANCOVA (e.g., Table 3, lines 2-3) are summarized in Tables 5 and 6. In all cases there was a significant linear relationship, but slopes did not differ significantly among the individual trials. Differences in the number of animals entrained in the flow during each disturbance (e.g., Table 3, line 2) result only in large standard errors associated with the mean y intercept. The lowest R^2 value (0.279) and poorest fit to the data ($p < 0.05$) occurred when Lone Oak was in full spate, well over bank full, and carrying out the experiment at all was difficult. On average, return rates (β) for the total invertebrates and Plecoptera were highest in Broadstone Stream, lowest in Dargall Lane and Green Burn, and intermediate in Lone Oak.

As expected, drift distances tended to increase and return rates to decrease with increasing velocity in any one channel, and streams with the highest velocities had the lowest return rates (Tables 5 and 6). There was no evidence of a temporal gradient associated with return rates. A power function has been used successfully (e.g., Elliott 1971; Ciborowski 1983; Iarkin and McKone 1985; Allan and Feifarek 1989) to describe the relationship between β and velocity (V):

$$\beta = aV^b \text{ or } \log \beta = \log a + b \log V$$

It is difficult to justify a similar statistical analysis of our data with only four experiments in each stream. Figure 3, however, shows a log-log plot of β versus V for the total invertebrate assemblage and the Plecoptera. The relationships are much the

same for both sets of taxa, and our data appear to be consistent with a power function. It is also apparent that (i) at a common velocity, return rates were highest in Broadstone Stream, lowest and similar in the Scottish sites, and intermediate in Lone Oak, and (ii) the relationship between return rate and velocity (slope of the line, b) differs among streams. Broadstone Stream showed the least change in return rate with increasing velocity; the slopes of the lines were similar and much steeper for the other three streams.

Although the data did not permit an extensive species by species analysis, some observations on individual taxa were possible. Figure 4 shows the relationship between the return rates of nemourid and leuctrid stoneflies in Broadstone Stream and Lone Oak. In Broadstone Stream, all the points on the graph are well below the 1:1 line, indicating that return rates of nemourids were lower than those of leuctrids. The data points for Lone Oak are closer to, and the error bars often overlap, the 1:1 line, indicating that return rates for these two families did not differ in this stream. As a corollary of this, the return rates of *Leuctra* spp. observed on the four occasions in Broadstone Stream tended to be higher than the four observed in Lone Oak for the same species (Fig. 4). The return rates for Nemouridae in the same trials, however, did not obviously differ between the streams.

Discussion

This study is the first attempt to relate the distances drifted by invertebrates to the hydraulic transport properties of stream channels. Few sites are suitable for such experiments, as transient storage properties have been assessed in only a few stony streams (Lancaster and Hildrew 1993), and for comparative purposes, sites with broadly similar species composition were

Table 5. Summary of mean velocity, stream discharge, experiment dates, slope (return rate), and y intercept of the regression equations, and statistical analyses (see text for details) for the total invertebrate assemblage.

Stream	Mean velocity (cm s ⁻¹)	Discharge (m ³ s ⁻¹)	Date	Return rate (β)	y intercept (α)	R ²	df	F	p
Broadstone Stream	10±3	0.016	93-04-04	0.360±0.051	5.25±0.21	0.684	1.23	49.801	<0.001
	12±3	0.012	93-05-11	0.377±0.050	5.38±0.21	0.710	1.23	56.186	<0.001
	14±3	0.009	92-10-19	0.339±0.061	6.46±0.26	0.608	1.20	31.077	<0.001
Lone Oak	36±3	0.039	92-11-16	0.334±0.057	6.54±0.24	0.622	1.21	34.579	<0.001
	27±4	0.016	93-05-06	0.273±0.066	5.08±0.27	0.430	1.23	17.334	<0.001
	31±4	0.019	92-11-09	0.258±0.050	5.27±0.21	0.539	1.23	26.940	<0.001
	44±5	0.062	92-11-30	0.215±0.039	5.18±0.16	0.567	1.23	30.117	<0.001
	89±8	0.295	93-04-05	0.108±0.036	6.69±0.15	0.279	1.23	8.916	<0.05
Green Burn	24±2	0.040	93-03-27	0.137±0.013	7.33±0.18	0.902	4.20	3.565	<0.05
							1.20	117.267	<0.001
							4.20	0.743	ns
	39±6	0.062	93-02-06	0.136±0.016	7.81±0.20	0.765	3.16	5.989	<0.01
							1.16	70.643	<0.001
							3.16	0.858	ns
	40±4	0.059	93-03-22	0.100±0.009	7.60±0.13	0.886	4.20	2.361	ns
							1.20	125.705	<0.001
							4.20	0.546	ns
	61±8	0.259	93-03-29	0.033±0.004	8.31±0.07	0.805	4.20	3.592	<0.05
Dargall Lane							1.20	48.783	<0.001
							4.20	0.349	ns
	30±2	0.071	93-03-22	0.120±0.014	6.30±0.21	0.796	4.20	0.177	ns
							1.20	68.728	<0.001
							4.20	0.687	ns
	31±3	0.065	93-03-27	0.122±0.015	6.35±0.18	0.844	4.20	1.827	ns
							1.20	91.003	<0.001
							4.20	1.514	ns
	40±3	0.081	93-02-08	0.115±0.016	6.54±0.20	0.781	3.16	1.567	ns
							1.16	51.763	<0.001
							3.16	1.152	ns
	40±3	0.081	93-02-03	0.100±0.028	6.88±0.18	0.309	1.28	12.500	<0.001

Note: Values are given as the mean ± 1 SE. R² refers to the coefficient of determination for the statistical models, ns indicates $p > 0.05$.

required. The limitation to only four sites restricts our ability to link invertebrate transport unequivocally with particular hydraulic conditions. Conversely, the hydraulic model fits the streams very well and there is a wealth of background quantitative information on invertebrate drift (McLay 1970; Elliott 1971; Ciborowski 1983; Campbell 1985; Larkin and McKone 1985; Allan and Feifarek 1989, and many others) against which we can look for patterns in our data. Nevertheless, results must be interpreted within these limitations.

There was no evidence of a temporal gradient associated with return rates, even though we carried out experiments between October and May. In Lone Oak, for example, the lowest and highest return rates were observed in spring experiments, whereas intermediate values occurred in autumn. In these months, temperatures in these streams are low and fluctuations small. Madsen (1968) did report decreased reaction times of heptageniid mayfly nymphs between being released into the drift and their obtaining a foothold on the substratum, but only after a substantial rise in temperature from 4 to 14 °C. Further, Elliott (1971) observed no variation in species return rates as a result of seasonal changes, including water temperature, between February and June in a northern English stream. Seasonal growth of aquatic macrophytes can also influence

drift distances (Elliott 1971) and could similarly have compromised our experiments, but no aquatic higher plants were seen in any of the streams. Dense growths of filamentous macroalgae can occur in the two Scottish streams in summer but did not during the experimental period. Therefore, it is unlikely that temporal or seasonal variations in environmental parameters among the experiments influenced our observations. There were virtually no seasonal shifts in the species composition or relative abundance in any of the four streams. We cannot exclude the possibility, however, of ontogenetic- or size-dependent shifts in drifting behaviour among seasons, as observed, for example, in some mayflies (Campbell 1985; Allan and Feifarek 1989).

The negative exponential model of invertebrate drift provided a reasonable description of the data relating drift catches to distance travelled from the source of the disturbance, as described by others (McLay 1970; Elliott 1971; Ciborowski 1983; Larkin and McKone 1985; Allan and Feifarek 1989). Comparisons of the drift return rates of the total and plecopteran species assemblages among streams were possible because the species composition was broadly the same in all sites. Although there is no a priori reason to expect even con-

Table 6. Summary of mean velocity, slope (return rate), and y intercept of the regression equations for the Plecoptera, and summary statistic associated with various analyses

Stream	Mean velocity (cm s ⁻¹)	Return rate (β)	y intercept (a)	R^2	df	F	p
Broadstone Stream	10	0.382±0.049	5.01±0.20	0.728	1.23	61.452	<0.001
	12	0.311±0.051	4.40±0.21	0.622	1.23	37.914	<0.001
	13	0.326±0.057	6.10±0.24	0.617	1.20	32.279	<0.001
	36	0.305±0.071	6.19±0.30	0.557	1.21	26.377	<0.001
Lone Oak	27	0.291±0.046	3.88±0.19	0.630	1.23	39.205	<0.001
	31	0.268±0.058	4.88±0.24	0.480	1.23	21.219	<0.001
	44	0.234±0.036	5.00±0.15	0.641	1.23	41.154	<0.001
	89	0.103±0.029	5.77±0.12	0.349	1.23	12.355	<0.01
Green Burn	24	0.155±0.018	7.19±0.22	0.882	4.20	1.406	ns
					1.20	100.447	<0.001
					4.20	1.503	ns
	39	0.145±0.017	7.73±0.22	0.855	3.16	5.278	<0.01
					1.16	67.939	<0.001
					3.16	0.651	ns
	40	0.101±0.010	7.39±0.14	0.870	4.20	2.061	ns
					1.20	106.142	<0.001
					4.20	0.383	ns
	61	0.031±0.004	8.15±0.06	0.829	4.20	6.689	<0.001
Dargall Lane					1.20	49.905	<0.001
					4.20	0.666	ns
	30	0.142±0.013	6.11±0.18	0.866	4.20	0.327	ns
					1.20	117.194	<0.001
					4.20	0.819	ns
	31	0.144±0.033	6.05±0.21	0.823	4.20	1.652	ns
					1.20	83.815	<0.001
					4.20	1.514	ns
	40	0.119±0.018	6.14±0.22	0.755	3.16	1.035	ns
					1.16	45.276	<0.001
					3.16	1.141	ns
	40	0.137±0.032	6.76±0.20	0.401	1.28	18.768	<0.001

Note: Values are given as the mean ± 1 SE. Discharges, dates, and other details as in Table 5. R^2 refers to the coefficient of determination for the statistical models. ns indicate $p > 0.05$.

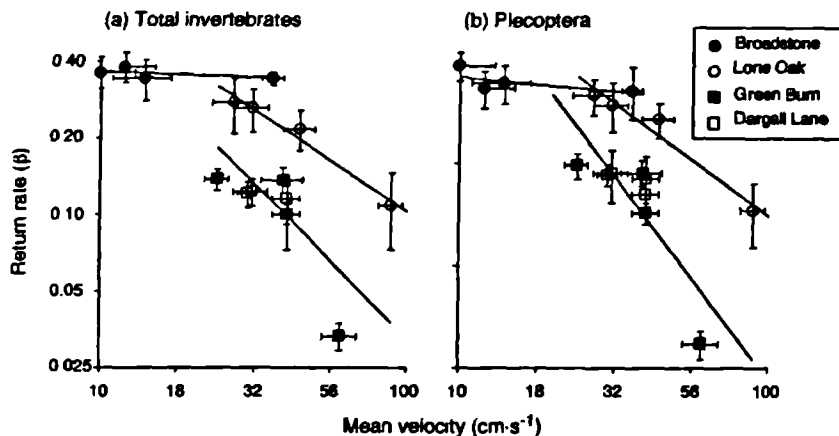
(1986) observed that drift behaviours were more similar within than between the orders Plecoptera, Ephemeroptera, and Trichoptera. All our streams were dominated by insects in the same order, Plecoptera, and mainly members of two families, the Nemouridae and Leuctridae.

Benthic macroinvertebrates do have distinct species- and size-specific return rates, however (McLay 1970; Elliott 1971; Campbell 1985; Allan and Feifarek 1989), and why these models fit multispecies assemblages so well is an interesting question. Larkin and McKone (1985) suggested that "the simple exponential is as good a fit as any to a hodge podge of phenomena and there is little point in trying to be more profound." This seems a rather defeatist stance and provides no insight into why return rates should differ between channels at similar current velocity and with similar species compositions. It is more likely that the return rates (or drift distances) of the entire assemblage are an average of the component species' return rates, weighted by their relative abundance in the community and constrained by channel hydraulics. In addition, the drift behaviour of species locally available to colonize a particular site may be a factor in determining their presence or absence. Only those species able to reduce downstream dis-

placement under prevailing conditions of discharge, fluvial morphology, and hydraulic storage are able to colonize and persist. Presumably, this is achieved by a limited set of behaviours, phenotypes, and morphologies making up species traits (Resh et al. 1994; Townsend and Hildrew 1994) that result in similar drift characteristics. Thus, the hydraulic habitat may partly determine patterns of species composition among streams, which have hitherto been ascribed overwhelmingly to chemical differences (e.g., Townsend et al. 1983). Perhaps it is not so surprising that the drift behaviour of whole assemblages can be described so well by a single model.

The return rates of the two stonefly families, Leuctridae and Nemouridae, varied relative to one another in two streams, at least under the range of our experimental conditions. The two families had similar return rates in Lone Oak, but the leuctrids had higher return rates than the nemourids in Broadstone Stream. These streams have virtually identical species assemblages, although relative abundances do differ and contrasting hydraulics could provide an explanation for these faunal differences. More interestingly, there is the possibility that species behaviours while in the drift (i.e., changes in body posture and type and amount of swimming (Madsen 1969

Fig. 3. Plot of return rates of (a) the total invertebrate assemblage and (b) the Plecoptera with respect to mean velocity in the four streams. Note that all axes are logarithmic. Lines are power functions, fit by eye. For simplicity, the two Scottish streams (Dargall Lane and Green Burn) have been treated as one.

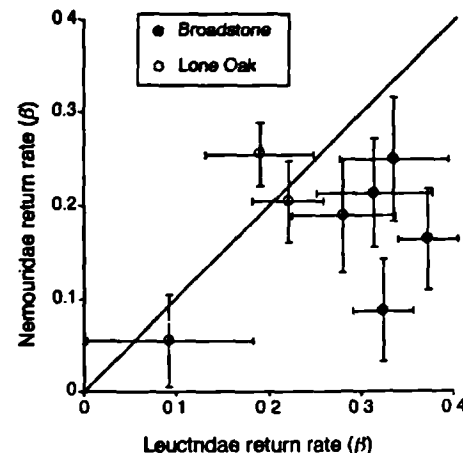


Otto and Sjöström 1986; Blum 1989)) vary with hydraulic conditions and hence influence their dispersal and colonization abilities. By altering their behaviour, some invertebrates can decrease drift time in response to high velocities (Allan and Feifarek 1989) or increase drift times at very low velocities (Minshall and Winger 1968; Poff and Ward 1991). Ciborowski (1983) observed similar return rates for the mayflies *Baetis tricaudatus* Dodds and *Ephemerella inermis* Eaton at low velocities, but at higher velocities, return rates for *E. inermis* were lower than for *B. tricaudatus*. A colonization experiment in Broadstone Stream (Lancaster et al. 1990) indicated that the nemourid *Nemurella pictetii* was a highly mobile, rapid colonist, whereas *Leuctra nigra* was a poor disperser and slow colonizer. This is consistent with our observations in the same stream that nemourids have lower return rates and higher drift distances than leuctrids, hence making them better colonizers.

Broadstone Stream and Lone Oak have different hydraulic properties, the former having a high dispersive fraction and lower mean velocity. The drift responses of leuctrid stoneflies appeared to reflect these physical differences in that the leuctrids drifted further in Lone Oak, whereas nemourid stoneflies had similar return rates in the two streams. This further suggests that drift may be under behavioural control in the leuctrids but more physically determined in the nemourids. Further elucidation of these differences between *Nemurella pictetii* and *Leuctra nigra* awaits future behavioural studies.

Our observations for the total invertebrate and stonefly assemblages are consistent with the hypothesis that invertebrate drift patterns are partly related to the hydraulic transport properties of stream channels. Return rates tended to be highest in streams with low mean velocities, and they also decreased with increasing velocity in any individual streams in a manner consistent with a log-log relationship, as found in other studies (Elliott 1971; Ciborowski 1983; Allan and Feifarek 1989). We did not encounter velocities so low ($<10 \text{ cm} \cdot \text{s}^{-1}$) that they prolonged drift (Minshall and Winger 1968; Poff and Ward 1991). More interestingly, β differed among streams at a com-

Fig. 4. Plot of return rates (mean $\pm 1 \text{ SE}$) of nemourid and leuctrid stoneflies found in four experiments each in Broadstone Stream and Lone Oak. Standard error bars for the Nemouridae and *Leuctra* spp. are in the x and y directions, respectively. The straight line represents a 1:1 relationship.



mon velocity, and the slope of the power function between β and V appeared to differ among streams. These differences seem to be attributable to different channel morphologies and transport properties. Return rates were highest, and varied least with velocity, in the stream with the highest dispersive fraction (Broadstone Stream), whereas return rates were lower, and decreased markedly with increased velocity, in the streams with low dispersive fractions (Green Burn, Dargall Lane, and Lone Oak).

It is not clear, however, why the three streams with similar dispersive fractions, and a similar relationship between return rates on velocity, should have different β values at a common velocity yet return rates in the Lone Oak are clearly

greater than those in the upland Green Burn and Dargall Lane. The explanation may be linked to differences in stream depth and (or) turbulence. Green Burn and Dargall Lane are approximately twice as deep as Lone Oak (Table 1). Reynolds et al. (1990) found that water depth was the controlling variable determining the rate of sinking loss for *Lycopodium* spp. spores in experimental channels, essentially because particles are transported further downstream in the time taken to sink through deeper water columns. This simple explanation may hold if the particle shape is such that the mean motion itself exerts no lift force, which would help maintain suspension (Smith 1975). The bodies of few benthic invertebrates are so simple in form, however, and reanalysis of our data including the vertical distance travelled by invertebrates did not alter return rates. It is possible that differences in turbulence, combined with depth, may play a role in determining β values (Elliott 1971; Ciborowski 1983). Allan and Feifarek (1989) suggested that Elliott (1971) estimated higher drift distances of *Baetis* spp. in a natural stream channel than they did in a laboratory flume, despite a similar dependence of distance travelled on velocity, because Elliott's natural channel had higher turbulence and a deeper water column. Clearly more investigations into the interactive effects of turbulence and depth on invertebrate drift are necessary.

High flow events and their associated high hydraulic forces are obvious sources of disturbance to benthic stream communities, and density-independent population losses may occur when individuals are transported out of the reach suitable for them. The results of this and many other studies suggest that once animals are entrained in the drift, losses will increase in all streams simply with increased velocity. The magnitude of the losses, and the rate of change with increased discharge, might vary among stream channels, however, in accordance with their hydraulic transport properties. Our results from this small sample of streams are consistent with this view. The dispersive fraction appears to be a useful hydraulic parameter to predict at least some of these patterns: animals in streams with low dispersive fractions may be most vulnerable to transport loss, especially during spates. Physically heterogeneous stream channels may impart resilience and resistance to indigenous communities, and the alteration of hydraulic transport properties may be one mechanism by which human simplification of river channels influences river ecosystems.

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Appendix 2. Species & Traits matrix for species where information was available. This matrix was divided into two for the analyses; one with reproductive traits only, and one with morphology traits only. Traits are given binary coding. For explanation of species names and traits, see Tables 6.6 and 6.7 respectively.

	a1	a2	b1	b2	c1	c2	d1	d2	e1	e2	f1	f2	g1	g2	h1	h2	j1	j2	k1	k2	k3	k4	m1	m2	n1	n2	n3	n4	n5	n6	n7	p1	p2	r1	r2	
chi		1		1	1		1			1	1			1		1		1			1	1	1						1			1				
sim		1	1		1		1			1	1		1			1		1			1	1								1		1				
cer	1		1																		1	1							1				1			
tip	1		1			1	1			1	1			1		1	1				1		1			1		1					1			
ped	1		1																		1									1				1		
dic	1		1																		1		1			1							1			
dix	1		1																		1			1						1			1			
atx	1		1																		1								1				1			
nem		1	1		1		1			1	1		1		1			1		1			1				1				1		1			
leu		1	1		1		1			1		1		1	1		1		1				1				1						1			
sit		1	1		1		1			1		1		1		1		1	1				1				1						1			
isg	1		1		1			1		1	1			1		1	1			1	1		1				1						1			
cab		1	1				1			1	1		1		1		1			1							1							1		
plc	1		1		1			1	1			1	1			1	1				1	1							1				1	1		
pol	1		1		1																1	1							1				1	1		
tin	1		1																		1	1							1				1			
lyp	1		1			1															1	1							1				1	1		
phm		1	1					1		1		1				1	1				1								1				1			
rhd	1		1		1			1	1			1		1		1	1			1			1				1						1			
agf		1	1		1			1		1		1		1		1	1			1		1		1					1				1			
hys	1		1		1			1		1		1		1		1	1			1	1								1	1			1	1		
lim	1		1																		1						1							1		
cha	1		1		1																1		1			1							1		1	
dra	1		1		1		1			1		1	1			1	1				1								1				1			
pot	1		1		1		1			1	1		1			1	1				1		1						1				1			
ste	1		1																		1		1						1				1			
stp	1		1		1			1		1	1		1			1	1				1		1						1				1			
ath	1		1		1			1		1	1		1			1	1				1		1			1							1		1	
mys		1	1		1		1			1	1		1			1	1				1		1			1							1		1	
oec		1		1	1		1		1			1		1		1	1				1		1			1				1			1		1	
brs	1		1		1		1			1	1		1			1	1				1		1						1				1			
bem		1	1		1		1			1	1		1			1	1				1		1						1				1		1	
sil		1	1		1															1				1		1							1		1	

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Appendix 2. (continued)

	a1	a2	b1	b2	c1	c2	d1	d2	e1	e2	f1	f2	g1	g2	h1	h2	j1	j2	k1	k2	k3	k4	m1	m2	n1	n2	n3	n4	n5	n6	n7	p1	p2	r1	r2
leh	1		1		1																1		1										1		1
epd	1		1		1		1			1	1			1	1			1			1		1						1				1		
epi		1	1		1			1		1	1			1	1			1			1		1			1					1				
bae		1		1		1	1			1	1			1		1		1	1		1		1		1							1			
cae		1	1			1	1			1	1			1	1			1			1		1				1					1			
lep		1	1				1			1		1		1		1		1			1						1								
haf		1			1																1		1				1					1			
pas	1		1		1																1		1		1		1		1				1		
hep		1	1																		1		1				1								
hes	1		1		1			1		1		1		1	1			1		1			1		1		1				1	1			
rhs		1	1		1			1		1		1		1	1			1		1			1				1				1	1			
ecd	1			1	1		1		1			1	1		1			1		1			1		1		1				1	1			
hyc	1		1		1		1			1		1	1			1		1				1			1	1							1		
ber		1	1		1																	1		1		1	1						1		
hyd		1	1		1															1				1			1	1	1				1		
lib		1	1		1																	1		1		1	1	1	1				1		
ela		1	1		1		1			1	1		1			1		1			1			1			1	1					1		
liv		1	1		1																	1		1			1	1					1		
out		1	1		1																	1		1			1	1					1		
stc		1	1		1		1			1						1		1			1						1	1					1		
agc		1	1		1			1		1		1	1		1			1	1							1	1	1					1		
cof	1		1		1		1			1		1		1		1		1	1							1	1	1					1		
orv		1	1		1		1			1		1	1		1		1		1					1		1	1						1		
cob	1		1		1		1	1				1	1		1			1			1			1					1				1		
sif	1		1		1				1	1				1		1	1		1				1				1					1			
anf		1	1																			1		1						1			1		
bit		1	1																			1		1						1			1		
pis		1	1																			1		1						1			1		
lym		1	1																			1		1			1						1		
gap	1		1																		1			1	1							1			
nia	1		1																		1			1	1							1			
ase	1		1																		1		1		1							1			
ost		1	1																			1		1					1				1		
hya		1	1																			1		1			1					1			
oli		1	1																			1		1					1			1			
hir	1		1																		1		1				1					1			
pla		1	1																		1		1				1					1			

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